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Neural architecture of selective stopping strategies – distinct brain activity patterns are associated with attentional capture but not with outright stopping

Running title: Brain activity in selective stopping strategies

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Abstract

In stimulus-selective stop-signal tasks, the salient stop signal needs attentional processing before genuine response inhibition is completed. Differential prefrontal involvement in attentional capture and response inhibition has been linked to the right inferior frontal junction (IFJ) and ventrolateral prefrontal cortex (VLPFC), respectively. Recently, it has been suggested that stimulus-selective stopping may be accomplished by different strategies: Individuals may selectively inhibit their response only upon detecting a stop signal (*Independent Discriminate then Stop strategy*) or unselectively whenever detecting a stop or attentional capture signal (*Stop then Discriminate strategy*). Alternatively, the discrimination process of the critical signal (stop vs. attentional capture signal) may interact with the go process (*Dependent Discriminate then Stop strategy*). Those different strategies might differentially involve attention- and stopping-related processes what might be implemented by divergent neural networks. This should lead to divergent activation patterns and, if disregarded, interfere with analyses in neuroimaging studies. To clarify this crucial issue, we studied 87 human participants of both sexes during a stimulus-selective stop-signal task and performed strategy-dependent functional magnetic resonance imaging analyses. We found that, irrespective of the strategy applied, outright stopping displayed indistinguishable brain activation patterns. However, during attentional capture different strategies resulted in divergent neural activation patterns with variable activation of right IFJ and bilateral VLPFC. In conclusion, the neural network involved in outright stopping is ubiquitous and independent of strategy while different strategies impact on attention-related processes and underlying neural network usage. Strategic differences should therefore be taken into account particularly when studying attention-related processes in stimulus-selective stopping.

Significance Statement

Dissociating inhibition from attention has been a major challenge for the cognitive neuroscience of executive functions. Selective stopping tasks have been instrumental in addressing this question. However, recent theoretical, cognitive and behavior research suggests that different strategies are applied in successful execution of the task. The underlying strategy-dependent neural networks might differ substantially. Here, we show evidence that, regardless of the strategy used, the neural network involved in outright stopping is ubiquitous. However, significant differences can only be found in the attention-related processes underlying those different strategies. Thus, when studying attentional processing of salient stop signals, strategic differences should be considered. In contrast, the neural networks implementing outright stopping seem less or not at all affected by strategic differences.

Introduction

Isolating neural underpinnings of response inhibition from those of attentional capture has been a key issue in the study of executive functions in recent years (Aron et al. 2014, 2015; Hampshire and Sharp, 2015a,b). Modified, stimulus-selective stop-signal tasks (SST) have been instrumental in dissociating neural underpinnings of attentional capture and response inhibition (e.g. Aron et al., 2007; Sharp et al., 2010; Boehler et al., 2011; Cai et al., 2011; Sebastian et al., 2016). The benefit of stimulus-selective over classical SSTs (Logan and Cowan, 1984) is that response inhibition is not conflated with the attentional capture of the stop signal, since go and stop signals are complemented by attentional capture (ac) signals which are matched to stop signals regarding to their stimulus features but require no response inhibition. Using such a stimulus-selective SST, we recently demonstrated distinct prefrontal involvement of right inferior frontal gyrus (IFG)/ anterior insula and inferior frontal junction (IFJ) in response inhibition and attentional capture, respectively (Sebastian et al., 2016).

In a recent behavioral study, Bissett and Logan (2014) showed that stimulus-selective SSTs are accomplished by different strategies. This might complicate disentangling neural networks involved in response inhibition and attentional capture. The commonly presumed strategy for performing a stimulus-selective SST is that participants first discriminate the critical signal and then cancel their response only if the signal was identified as a stop signal. Otherwise, they finish the go process without ever initiating an inhibitory process. Since individuals stop only after discriminating stop signals as such, inhibitory and attention-related processes are fully independent (*Independent Discriminate then Stop strategy, ID)*. However, participants employing the *Stop then Discriminate strategy (SD)* unselectively inhibit their response upon appearance of any critical signal. They then discriminate the signal and decide whether to complete the stop process (stop signal) or to restart the go process (ac signal). Hence, inhibitory processes should not only be present on stop but also on ac trials. In the third strategy, the *Dependent Discriminate then Stop strategy (DD)*, the requirement to

discriminate stop and ac signals interacts with the go process thereby slowing go reaction time whenever a critical signal is displayed. This has crucial implications for estimating the stop-signal reaction time (SSRT), which is the measure of stopping capability in a SST (cf. Bissett and Logan, 2014 for discussion).

How these three strategies impact on the neural activation patterns of attentional capture and response inhibition is not clear. Only when the strategies and underlying processes as well as related neural networks are understood selective SSTs can be used to separate stopping and attention-related neural activity. Bissett's and Logan's (2014) theoretical notions implicate that while in ID inhibitory and attention-related processes are fully independent, in SD inhibitory processes should also be present during ac trials, since individuals applying this strategy stop unselectively upon detecting any critical signal. Contrasting stop and ac trials to isolate the neural stopping from the attentional network may in turn dilute results in individuals using SD in a sense of subtracting at least some neural activation involved in stopping. Similarly, the dissociation of inhibitory and attentional networks in DD may be blurred due to the interaction of discrimination and go processes. Using functional magnetic resonance imaging (fMRI) we addressed the important and still open question whether neural networks involved in stopping and attentional capture show strategy-dependent divergent action patterns. If strategy-dependent brain activation patterns existed, different stopping strategies should be appreciated in future neuroimaging studies that aim at differentiating the neural underpinnings of response inhibition and attention. We expected a clear dissociation of neural underpinnings of stopping and attentional capture only in ID. SD was hypothesized to be associated with enhanced right IFG activity during ac and attenuated right IFG activity during stopping. DD was expected to show altered network activity due to the interaction of discrimination and go processes.

Materials and Methods

Participants

In total, 87 healthy human participants participated in the study. One participant had to be excluded due to excessive head movement (>2 mm) inside the scanner and another six for not following the task instructions. The remaining 80 participants (49 female, 31 male) had a mean age of 24.8 years (SD = 4.1, range = 20–47 years). All individual participants included in the study were screened for factors contradicting MRI scanning and provided written informed consent prior to participation. They were all right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected to normal vision and were free of psychotropic medication. None of the participants had a history or current evidence of psychiatric or neurological diseases. The study was approved by the local ethics committee and participants were financially compensated for their time. The analyses and results of the initial, smaller sample (n=28) have previously been published elsewhere (Sebastian et al., 2016). While the previous study focused on the dissociation of attentional and response inhibition networks of dorsal and ventral areas of the right inferior frontal cortex independent of potential strategies to perform a selective SST, the current study aimed at identifying strategy-dependent differences in neural circuits involved in outright stopping and attentional capture. Therefore, this initial sample was extended to gain reasonable sample sizes for each strategy.

Experimental design

Paradigm: We employed a stimulus-selective SST (Fig. 1, see also Sebastian et al., 2016) using Presentation software (version 18.0, www.neurobs.com). Before the scanning session, participants received a brief training session on a laptop computer to make sure that the participants correctly understood the task instructions and to familiarize them with the task prior to the scanning session. All participants accomplished three runs of the selective SST during the scanning session.

--- please insert figure 1 here ---

Throughout scanning, participants were asked to hold an MR compatible response button box in their hands and to respond to the stimuli by pressing a response button with the left or right index finger. Prior to the beginning of each run, instructions were given orally. Instructions equally stressed speed and accuracy of responding.

The task comprised three conditions: a go condition (50 %), a stop condition (25 %), and an ac condition (25 %). At the beginning of each trial, a white fixation cross was presented in the center of the screen for 500ms. Then a white arrow was displayed for 1,000 ms (equivalent to the maximum permitted reaction time) or until a button press was performed. Participants were instructed to respond corresponding to the pointing direction of an arrow (i.e., left index finger button press for an arrow pointing to the left and a right index finger button press for an arrow pointing to the right). In case of a button press the arrow vanished and the screen remained blank until the end of the trial.

In the stop condition, the arrow changed its color from white to blue after a variable stop-signal delay (SSD). Participants were instructed to try canceling the response in case of a stop signal. The SSD was adapted to the participants' performance following a staircase procedure to yield a probability of 50% of successful response inhibitions per run. The initial SSD was set to 210ms. If the response was not successfully inhibited (commission error), the SSD in the next stop trial was decreased by 30ms with a minimum SSD of 40ms. If a response was successfully inhibited (successful stop), the SSD in the next stop trial was increased by 30ms. The maximum SSD was limited by the maximum permitted reaction time.

In the ac condition, the arrow changed its color from white to green after a variable ac signal delay (ASD) following the onset of the arrow. Participants were instructed to continue their response in case of an ac signal. The ASD was varied in accordance with the staircase in the stop condition. The attribution of color (green/blue) to trial type (stop/ac) was counterbalanced across participants.

In case of an omission error (no button press) in the go or ac condition, participants were given a short feedback (''oops—no button press'' for 500ms) to maintain the participants'

attention and to limit proactive slowing. The length of the intertrial interval was varied randomly between 2,500 and 3,500ms. Presentation of fixation cross, arrow and intertrial interval added up to an average trial duration of 4,500ms. One run consisted of 112 trials presented in a randomized order.

Statistical analyses

Behavioral data analyses: Behavioral data (reaction time (RT) and accuracy) were collected by the Presentation software and analyzed using SPSS® software (IBM® SPSS® version 23). Measures of interest were mean RT on correct go and correct ac trials as well as on unsuccessful stop trials, and percentage of errors (i.e., incorrect go trials, commission errors on stop trials, and omission errors on go and ac trials). The SSRT was computed using the integration method which has been shown to be less susceptible to the shape of the RT distribution than the mean method (Verbruggen et al., 2013). Since the validity of the SSRT estimation rests on the assumption of context independence (Logan and Cowan, 1984) which is violated in DD, Bissett and Logan (2014) suggested the use of the ac RT distribution as an estimate of the underlying go distribution on stop trials. For the sake of completeness, we computed the SSRT once based on the go RT distribution for all groups and once based on the ac RT distribution as the underlying go RT distribution for participants using the DD strategy. The former approach was only taken for the sake of completeness despite being invalid since the assumption of context independence underlying valid SSRT estimation (Logan and Cowan, 1984) is violated in DD. The latter approach requires the strong assumption that the dependence between going and signal processing is the same on stop and ac trials which remains to be validated (Bissett and Logan, 2014). We did not compute the SSRT based on ac RT distribution for ID and SD as for these strategies context independence is given. Given these preconditions comparisons of SSRT between DD and both other strategies should be interpreted with caution and should be viewed as a first approximation.

Stimulus-selective stopping strategies: Three selective stopping strategies were defined following Bissett and Logan (2014) (see also decision matrix in Fig. 2 that was used for strategy assignment of each participant): (1) Independent Discriminate then Stop strategy (ID): If a critical signal is shown (i.e., a blue or green arrow), participants may discriminate the signal before deciding whether or not to stop their response. If the signal is identified as a stop signal, they stop; otherwise they complete the go process without ever initiating the stop process. Hence, RT in ac trials should not be longer compared to go RT. However, as context independence is assumed in this case, i.e., that the finishing time of the go-process is unaffected by the presence of a stop signal, RT in unsuccessful stop trials should be faster compared to go trials; (2) Stop then Discriminate strategy (SD): Participants may inhibit their response upon any critical signal being displayed, and then discriminate the signal to decide whether or not to respond. If the signal is a stop signal, they stop; otherwise they restart the go process. Therefore, RT in ac trials should be longer than in go trials, whereas RT in unsuccessful stop trials should be faster compared to go trials due to assumed context independence; (3) Dependent Discriminate then Stop strategy (DD): The requirement to discriminate stop and ac signals may interact with the go process. RT will consequently be slowed down whenever a critical signal is detected resulting in RT in unsuccessful stop trials which are not shorter than go RT whereas RT in ac trials should be longer than in go trials. The dependency violates the assumptions of the independent race model.

--- please insert figure 2 here ---

To classify each participant, we followed the procedure described by Bissett and Logan (2014). In short, mean RT for go, ac, and unsuccessful stop trials were compared for each participant and the implicated strategy was assigned. To compare the evidence for and against the null hypotheses without bias, Bayes factor, which is the ratio of the odds in favor of the null hypothesis to the odds in favor of the alternative hypothesis, was used (Rouder et al., 2009). A Bayes factor of 1 indicates that the odds in favor of the null hypothesis are no better than the odds against it. Numbers greater than 1 support the null hypothesis, whereas

numbers less than 1 support the alternative hypothesis. In accordance with Bissett and Logan (2014), we therefore accepted the null hypothesis when the Bayes factor was greater than 1 and accepted the alternative hypothesis when the Bayes factor was less than 1. In comparing stop RT and go RT, we only accepted the alternative hypothesis if stop RT was faster than go RT. The Bayes factor was calculated by calculating the mean and standard deviation of go RT, ac RT, unsuccessful stop RT separately for each participant. Then, go RT and unsuccessful stop RT as well as go RT and ac RT were compared in two independent samples *t*-tests. To convert *t*-tests and sample sizes to Bayes factors, we used Jeff Rouder's Bayes factor calculator on the Perception and Cognition Lab website (http://pcl.missouri.edu/bf-two-sample) with the recommended Jeffrey-Zellner-Slow Prior with the default value of 1, which is appropriate if there are no strong prior assumptions (Rouder et al., 2009).

MRI Data Acquisition: Images were acquired on a Magnetom Trio syngo 3 T system (Siemens, Germany) at two sites, equipped with an 8-channel head coil at site 1 and a 32-channel head coil at site 2 for signal reception. Stimuli were projected on a screen at the head end of the scanner bore and were viewed with the aid of a mirror mounted on the head coil. Foam padding was used to limit head motion within the coil. A high-resolution T1-weighted anatomical data set was obtained using a 3D magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence for registration purposes (site 1: TR = 2,250 ms, TE = 2.6 ms, flip angle = 9°, FOV = 256 mm, 176 sagittal slices, voxel size 1×1×1 mm^3; site 2: TR = 1,900 ms, TE = 2.52 ms, flip angle = 9°, FOV = 256 mm, 176 sagittal slices, voxel size 1×1×1 mm^3). Functional MRI images were obtained using T2*-weighted echo-planar imaging (EPI) sequence (both sites: TR = 2,500 ms, TE = 30 ms, flip angle = 90°, FOV = 192 mm, 36 slices, voxel size = 3×3×3 mm^3).

Preprocessing of fMRI data: SPM12 (www.fil.ion.ucl.ac.uk/spm/software/spm12/) was used to conduct all image preprocessing and statistical analyses, running with Matlab 2013b (The Mathworks Inc., Natick, Massachusetts, USA). Images were screened for motion artifacts

prior to data analysis. Excessive head motion (>2 mm) was observed in one of the participants' who was consequently excluded from all data analyses. Next, images were manually reoriented to the T1 template of SPM. The first five functional images of each run were discarded to allow for equilibrium effects. Then, several preprocessing steps were carried out on the remaining functional images. First, images were realigned to the first image of the first run, using a six degrees-of-freedom rigid body transformation. The realigned functional images were co-registered to the individual anatomical T1 image using affine transformations. Subsequently, the anatomical image was spatially normalized (linear and nonlinear transformations) into the reference system of the Montreal Neurological Institute's (MNI) reference brain using standard templates, and normalization parameters were applied to all functional images. Finally, the normalized functional data were smoothed with a three-dimensional isotropic Gaussian kernel (8 mm full width at half maximum) to enhance signal-to-noise ratio and to allow for residual differences in functional neuroanatomy between subjects.

Single subject analysis: A linear regression model (general linear model, GLM) was fitted to the fMRI data of each subject. All events were modeled as stick functions at stimulus onset and convolved with a canonical hemodynamic response function. The model included a high-pass filter with a cut-off period of 128 s to remove drifts or other low-frequency artifacts in the time series. After convolution with a canonical hemodynamic response function, three event types were modeled as regressors of interest: correct go, successful stop, and correct ac trials. Incorrect reactions for each condition and omission error feedback were modeled as regressors of no interest. In addition, the six covariates containing the realignment parameters capturing the participants' movements during the experiment were included in the model.

Group analysis: We compared neural activation patterns of the three groups, i.e. ID, SD, and DD during outright stopping (successful stop vs. correct ac, stop>ac) as well as during attentional capture (correct ac vs. correct go, ac>go) using separate fullfactorial models with

group as between factor (ID, SD, DD). Scanning site was entered as a covariate of no interest. Significant effects for each condition were assessed using *t*-statistics. The respective group results were thresholded at $p<0.05$ corrected for multiple comparisons (family wise error, FWE, correction at peak level) and k = 5 contiguous voxels. The SPM anatomy toolbox 2.0 (Eickhoff et al., 2007) was used to allocate significant clusters of activation to anatomical regions.

Region of interest analysis: In order to further test our hypotheses regarding distinct strategy dependent prefrontal involvement in outright stopping and attentional capture, we performed a region of interest (ROI) analysis. We were specifically interested in four prefrontal regions that have commonly been associated with response inhibition and attentional capture, i.e. bilateral IFG/ anterior insula, pre-supplemental motor area (pre-SMA), and right IFJ (Levy and Wagner, 2011; Swick et al., 2011; Sebastian et al., 2013; Cai et al., 2014). Since ROI analyses should only be performed in truly active regions (Kriegeskorte et al., 2009), we employed a *t*-contrast thresholded at $p_{FWE}<0.001$ that tested the average of stopping and attentional capture against simple going (following Boehler et al., 2011) independent of the strategy applied. This contrast revealed widespread and robust activation. The center of the 5-mm-radius spherical ROIs was then anatomically derived by choosing peaks of significantly activated clusters within bilateral IFG/ anterior insula (right IFG/ anterior insula: x=44, y=22, z=-6; left IFG/ anterior insula: x=-34, y=20, z=-4), pre-SMA (x=6, y=22, z=46), and right IFJ (x=42, y=10, z=42). RFX plot (Gläscher, 2009) was used to extract contrast estimates from individual peaks within each ROI for outright stopping (stop>ac) and attentional capture (ac>go). Separate one-way analyses of variance (ANOVAs) of the extracted contrast estimates were used for statistical assessment with group (ID, SD, DD) as between factor. In addition to the classical ANOVAs we computed Bayesian ANOVAs (Rouder et al., 2016; Rouder et al., 2012; Rouder et al., 2017; Wetzels et al., 2012) using JASP (JASP Team, 2017; Version 0.8.1.2; https://jasp-stats.org/). The prior width of the Cauchy prior for the model parameters was kept at the default setting of 0.5. One of the benefits of Bayesian statistics is that it provides evidence favoring the null (i.e., that there is

no difference, BF_{01}) as well as the alternative hypothesis (i.e., that there is a difference, BF_{10}) (e.g. Gallistel, 2009; Wagenmakers et al., 2016). Combining the results of frequentist and Bayesian approaches increases the confidence that the overall conclusion is robust if both results point in the same direction (Wagenmakers et al., 2017).

Results

Behavioral data

Participants performed accurately as indicated by low error rates on go and ac trials. Commission error rate of stop trials was close to 50 % indicating the adherence of the participants to the task rules and the successful operation of the staircase procedure (table 1). To control for an effect of attribution of color, the experiment was designed in a cross-balanced manner, i.e., the attribution of color (blue/green) to trial type (stop/ac) was balanced across participants. A univariate ANOVA with color as between factor revealed no group differences with respect to the stopping latency as measured by the SSRT, reaction times (RT go, ac, unsuccessful stop) or error rates (stop commission errors, incorrect go, go or ac omission errors) (all $p>0.5$).

Each participant was individually assigned to one of the selective stopping strategies by comparing their mean RTs for correct go, correct ac, and unsuccessful stop trials as described above (Bissett and Logan, 2014). Eighteen participants were assigned to the ID strategy, 31 participants used the SD strategy and 27 participants were characterized as applying the DD strategy. The remaining four participants could not be assigned to one of the selective stopping strategies and were excluded from further analyses. Strategy specific behavioral data are given in table 1.

--- please insert table 1 here ---

We compared SSRT of the three strategies to test specific predictions about strategy specific differences in the stopping latency proposed by Bissett and Logan (2014). A one-way ANOVA with group as between factor resulted in a significant main effect of group on SSRT based on go RT as the underlying RT distribution ($F_{(2,73)} = 3.15$, $p=0.049$, $\eta^2=.080$, $BF_{10}=1.37$). Bonferroni-corrected post hoc comparisons revealed that SSRT was slower in DD as compared to SD ($p=0.046$) while SSRT did neither significantly differ between ID and DD ($p=1.00$) nor between ID and SD ($p=0.510$). When SSRT was based on ac RT as the underlying RT distribution for DD and on go RT as the underlying RT distribution for ID and SD since independence assumptions between stop and go process were preserved for ID and SD, a one-way ANOVA with group as between factor again resulted in a significant main effect of group on SSRT ($F_{(2,73)} = 11.16$, $p<0.001$, $\eta^2=.234$, $BF_{10}=9.86$). Bonferroni-corrected post hoc comparisons revealed that SSRT was slower in DD as compared to SD ($p<0.001$) and slower in DD as compared to ID ($p=0.028$).

Imaging data

We first assessed whether behavioral measurements of attention-related processes (i.e., RT change on ac vs. go trials) and outright stopping (i.e., SSRT) relate to the respective brain activation patterns within the present data set, particularly in right IFJ and bilateral IFG/ anterior insula as suggested by previous results (Sebastian et al., 2016). As seed voxels we chose peak voxels for attentional capture (ac > go) and outright stopping (stop > ac) which we identified within the ID group. We chose to specify the seeds within the ID group since the discrimination process and the stopping process should be unrelated in ID. The respective contrasts should therefore best reflect brain regions associated with the processes of interest. We then extracted activity estimates from volumes of interest with a radius of 5mm around these seeds (right IFJ: x=44, y=8, z=26; right IFG/anterior insula: x=44, y=18, z=-4; left IFG/anterior insula: x=-34, y=14, z=-6) for all participants. Subsequently, right IFJ activity estimates were correlated with RT change (ac RT – go RT) and bilateral IFG/ anterior insula activity estimates were correlated with SSRT values. This resulted in negative correlation of

RT change with right IFJ activity (Pearson's r= -.213, p=.032, one-sided test) and positive correlation of SSRT with bilateral IFG/ anterior insula activity (right: Pearson's r= .217, p=.030; left: Pearson's r= .226, p=.025; one-sided test) (Fig. 3). These correlations indicate that IFJ and IFG/ anterior insula are involved in attentional capture and implementation of stopping in the present sample. Brain activity within these regions can thus be viewed as markers of attention-related vs. inhibitory processes to the actual behavior in present dataset.

--- please insert figure 3 here ---

To compare neural underpinnings of attentional capture and outright stopping for the three selective stopping strategies we first preformed direct group comparisons. To further test the differential function of distinct prefrontal regions in selective stopping strategies, we performed a ROI analysis in four prefrontal ROIs, i.e., bilateral IFG/ anterior insula, pre-SMA, and right IFJ. We therefore evaluated the activation pattern (contrast estimates) in these ROIs during attentional capture (ac > go) and outright stopping (stop > ac) in the three selective stopping types using separate oneway ANOVAs with group (ID, SD, DD) as between factor.

Attentional capture depending on selective stopping strategies

Direct comparison of selective stopping strategies during attentional capture revealed significantly stronger activity in right IFJ for SD as compared to DD (x=38, y=14, z=40, Z=5.04, p_{FWE}=.008) (Fig. 4). All other whole brain comparisons of selective stopping strategies during attentional capture revealed no significant group differences.

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The more sensitive ROI analysis resulted in significant effects during attentional capture for right IFG/ anterior insula ($F_{(2,73)}$=4.99, p=.009, η^2=.120), left IFG/ anterior insula ($F_{(2,73)}$=8.60, p<.001, η^2=.191) and right IFJ ($F_{(2,73)}$=6.36, p=.003, η^2=.148), whereas the ROI analysis for pre-SMA was non-significant ($F_{(2,73)}$=1.69, p=.192, η^2=.044). Bonferroni corrected post-hoc t-

tests revealed that the SD group as compared to the DD group displayed significantly enhanced activity within bilateral IFG/ anterior insula (right: p=.008; left: p<.001) as well as in right IFJ (p=0.002). In addition, the SD group as compared to the ID group displayed significantly enhanced activity in right IFG/ anterior insula (p=.048). Similarly, Bayes factors resulting from the Bayesian approach provided strong and very strong evidence for the right IFJ and left IFG/anterior insula, respectively, as well as moderate evidence for the right IFG/ anterior insula that the data was 6, 78, and 15 times more likely to occur under the alternative hypothesis than under the null hypothesis, whereas no such evidence for the pre-SMA was revealed (Bayes factors are given in table 2). Results of the ROI analysis are depicted in Fig. 5a.

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Outright stopping depending on selective stopping strategies

Neither direct comparisons of selective stopping strategies nor ROI analyses (Fig. 5b) revealed significant group differences during outright stopping (stop > ac). More specifically, the non-significant results of the ANOVAs were as follows: right IFG/ anterior insula ($F_{(2,73)}$=0.22, p=.806, η^2=.006); left IFG/ anterior insula ($F_{(2,73)}$=0.74, p=.480, η^2=.020); right IFJ ($F_{(2,73)}$=1.05, p=.355, η^2=.028); pre-SMA ($F_{(2,73)}$=3.09, p=.051, η^2=.078). Again, the results using the Bayesian approach corroborated the results of the frequentist approach. Resulting Bayes factors provided moderate evidence that the data in bilateral IFG/anterior insula and right IFJ were 4 to 7 times more likely to occur under the null hypothesis than under the alternative hypothesis. For pre-SMA, the Bayes factor provides only anecdotal evidence that the data occurred more likely under the alternative hypothesis (Bayes factors are given in table 2).

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Discussion

We used direct group comparisons and region of interest (ROI) analyses to study the impact of stimulus-selective stopping strategies on brain activation patterns involved in attentional capture and outright stopping. While all groups displayed robust and indistinguishable brain activation patterns during stopping, strategy-dependent differences in prefrontal regions were present during attentional capture only.

As expected, the SD group displayed significantly enhanced activity in bilateral IFG/anterior insula during attentional capture and thus in regions commonly assigned to response inhibition (Aron, 2011; Levy and Wagner, 2011; Swick et al., 2011; Sebastian et al., 2013; Dambacher et al., 2014; Sebastian et al., 2016). Moreover, the right IFG/anterior insula was associated with SSRT in the present study. The finding of enhanced IFG/anterior insula is well in line with the theoretical view that individuals using the SD strategy stop unselectively upon any critical signal (Bissett and Logan, 2014). Accordingly, key regions of the response inhibition network were recruited on ac trials in individuals applying the SD strategy. In addition, attentional capture in SD was associated with increased IFJ activity as compared to the DD group. IFJ activity was presently associated with RT increase on ac trials and is presumed to be elevated when a salient signal indicates a change of the current action plan (Levy and Wagner, 2011; Sebastian et al., 2016). This finding thus adds neuroscientific evidence to the notion that participants using the SD strategy need to re-initiate the go-process after successfully identifying an ac signal as such. This should additionally involve heightened attentional processing to boost the go-process that presumably decays during the discrimination process in SD (Bissett and Logan, 2014) which is likely reflected in a fronto-parietal network including IFJ (Sebastian et al., 2016). As a consequence, it is plausible that right IFJ responds stronger in SD during attentional capture. Findings from a study using electroencephalography (Sánchez-Carmona et al., 2016) support this interpretation. In that study differences between stop and ac conditions in event related potentials in the P3 latency range occurred in SD only after the estimated SSRT and thus after the stopping process was completed whereas in DD P3-differences were observed before the estimated SSRT, hence during the stopping process. The authors suggest that the

absence of neurophysiological differences between stop and ac conditions before completion of the stopping process in SD support the theoretical notion of unselective stopping. In addition, P3-differences between stop and ac conditions after the completion of the stop process in SD might reflect differences in postprocessing steps including the re-initiation of the go response in case of ac-signals (Sánchez-Carmona et al., 2016). Those neurophysiological findings complement the present fMRI results well and reveal interesting insights in the neural timing of strategy-dependent selective stopping processes which cannot be captured by fMRI. Yet, it remains to be tested whether these electrophysiological findings truly reflect significantly different, strategy-specific patterns since event related potentials were not directly compared between strategies. Sánchez-Carmona et al. (2016) focused on the isolation of the stopping process itself (i.e., stop>ac). Yet, they did not directly assess whether strategy-dependent neurophysiological differences between ac and go trials were present. This is, however, crucial to directly test to for stopping related neural activity during attentional capture in SD. Findings from the study by Sánchez-Carmona et al. (2016) therefore serve rather as indirect evidence. Using the ac>go contrast as a function of strategies, we directly demonstrate significantly stronger activity in the stopping network in SD and thus direct evidence for unselective stopping specifically in SD. Taken together, findings from different imaging modalities demonstrate that in line with the theoretical notion of unselective stopping in SD, individuals applying this strategy recruit the neural network involved in response inhibition also on ac trials and rely on additional attention-related processes accompanied by enhanced IFJ activity to re-start the go-process, whereas activation patterns in ID and DD support the notion of selective stopping in those strategies.

Strikingly, for outright stopping significant group differences were neither observed in whole brain group contrasts nor in more sensitive ROI comparisons. The absence of group differences during stopping was further underlined by the Bayesian ANOVAs which revealed Bayes factors (BF_{10}) ranging between approximately 0.14 and 0.26 for bilateral IFG/ anterior insula and right IFJ suggesting that these data are 4 to 7 times more likely to be observed under the null hypothesis than under the alternative hypothesis. There was only inconclusive

472 evidence for differences in pre-SMA activity between selective stopping strategies. The
473 classical ANOVA for the pre-SMA just failed to reach significance and the Bayes factors
474 (BF_{10}=1.30) were rather indecisive (note that a Bayes factor of 1 may be interpreted as no
475 evidence and Bayes factors of 1-3 may be interpreted as anecdotal evidence; Jeffreys, 1961;
476 Wagenmakers et al., 2017). Given the present data evidence for differences in pre-SMA
477 activity may thus be viewed as rather weak. Most surprisingly, SD was not associated with
478 attenuated right IFG/ anterior insula activation during outright stopping as compared to ID
479 and DD. In line with Bissett and Logan (2014), we expected individuals using the SD strategy
480 to stop unselectively upon any critical signal before discriminating it as an ac or stop signal.
481 Accordingly, we had hypothesized that the SD group would show activation in networks
482 underlying response inhibition upon viewing stop as well as ac signals which in turn should
483 result in reduced brain activity in ventrolateral prefrontal regions when contrasting stop and
484 ac trials as compared to both other strategies. However, despite the fact that attentional
485 capture in SD was clearly associated with brain activation of regions critically involved in
486 response inhibition, brain activation patterns in SD did not significantly differ from both other
487 groups during outright stopping (Fig. 5b). This suggests that stopping upon detecting critical
488 signals in SD is rather consistent with a hesitation or shortly braking than a complete stop.
489 This fits well with the notion that the right inferior frontal cortex implements a brake which
490 may represent a partial form of stopping (Aron et al., 2015; Aron et al., 2014; Wessel and
491 Aron, 2014, 2017) probably facilitating subsequent stopping whereas activation of the
492 stopping network during outright stopping follows an “all-or-nothing-principle” which is
493 uniform across all strategies. In light of the previous literature the present results thus
494 suggest that participants using the SD strategy partially stop upon detecting critical signals in
495 selective stopping paradigms. Only if the signal is identified as a stop-signal, the stopping
496 process is completed thereby relying on the neural network involved in stopping like
497 participants using the ID or DD strategy.

498 Specifically the involvement of ventrolateral prefrontal regions in stopping tasks was subject
499 to debate in recent years. Some authors argued that the ventrolateral part of the inferior

frontal cortex is engaged in the detection and attentional processing of salient stimuli (Hampshire et al., 2010; Sharp et al., 2010) or in domain-general cognitive control mechanisms (e.g. Duncan, 2013; Erika-Florence et al., 2014; Swick and Chatham, 2014; Hampshire and Sharp, 2015b). Yet others ascribe a brake function to the VLPFC which may slow, pause, or completely cancel an action via fronto-basal-ganglia networks (Aron et al., 2015; Aron et al., 2014). Sharp and colleagues (2010) used a similar experimental paradigm as the one used in the present study. They reported not only right IFJ activity but also right IFG/anterior insula activity associated with attentional capture. Aron and colleagues (2014) argue that ac signals might function as a braking component triggering right IFG/anterior insula activity. More recently, a unifying theory has been suggested that a global suppressive fronto-basal-ganglia network including ventrolateral prefrontal cortex is generally recruited upon detecting any surprising events to briefly interrupt action and impact cognition (Wessel and Aron, 2017). This notion corresponds to the SD strategy proposed by Bissett and Logan (2014). In line with that view (Wessel and Aron, 2017), brain activity across all strategies reveals ventrolateral prefrontal activation for attentional capture (Fig. 5a). This supports the notion of salient, surprising signals being perceived as a braking signal (Aron et al., 2014; Wessel and Aron, 2017). Moreover, the present findings suggest individual differences in attentional capture of salient signals and subsequent braking as revealed by enhanced IFG/ anterior insula activity in SD during attentional capture. The degree of braking upon unexpected events thus seems highly variable given the strategy-dependent differences in ventrolateral prefrontal brain activity associated with attentional capture.

In order to test whether brain activity during attentional capture and outright stopping were related to behavioral measures we computed brain-behavior correlations. Indeed, IFJ activity during attentional capture negatively correlated with RT increase on ac trials. This suggests that individuals who engage IFJ more strongly are less susceptible to attentional capture. Interestingly, bilateral IFG/ anterior insula during outright stopping correlated positively with SSRT in the current sample indicating that individuals who have more difficulties to stop an ongoing response engage right IFG/ anterior insula more strongly. This finding contrasts with

previously reported negative correlations suggesting that stronger IFG/ anterior insula engagement might be associated with more efficient stopping (e.g. Aron and Poldrack, 2006; Aron et al., 2007; Boehler et al., 2012), while yet other studies failed to show such a relationship (Chao et al., 2009; Sharp et al., 2010). Two recent studies indirectly support the present finding. Hughes et al. (2013) showed that right IFG/ anterior insula engagement was related to stopping difficulty. In both within- and between-subject analyses right IFG/ anterior insula was more strongly activated during more difficult stopping. A positive relationship between SSRT and stopping-related brain activity was also reported by Zhang et al. (2015) who performed an independent component analysis of functional networks associated with outright stopping. In that study, activity in a functional network comprising the subthalamic nucleus amongst other regions correlated positively with SSRT during successful stopping. Of note, the subthalamic nucleus is part of the so-called hyper-direct pathway projecting from the prefrontal cortex to the subthalamic nucleus that has been linked to response inhibition (Aron 2011). Moreover, the subthalamic nucleus has recently been shown to be causally involved in interrupting behavior (Fife et al., 2017). Taken together, several studies including the present one provide converging evidence that stopping difficulty might be associated with stronger recruitment of a fronto-basal-ganglia network.

The three selective stopping strategies differed not only with respect to their neural activation patterns, but also regarding the SSRT. Fastest SSRT was found in SD, slowest SSRT was present in DD. These findings are in line with findings by Sánchez-Carmona and colleagues (2016) and support suggestions of Bissett and Logan (2014) that are based on the comparison of SSRT in selective and simple SSTs. They suggested that in ID, in which the stop process is initiated after the discrimination process, selective SSRT should be slowed down since the discrimination process of the signal is a slower process than simple signal detection (Donders, 1868/1969). Participants applying the SD strategy, however, do not stop selectively but unselectively upon any critical signal. As the stop process occurs before the discrimination process, selective SSRT should not differ from simple SSRT and should thus be faster than selective SSRT in ID. The present results are in line with this theoretical

556 notion. For the DD strategy Bissett and Logan (2014) expected the SSRT to be slow since
557 the individual engages a selective stopping mechanism involving an additional discrimination
558 stage. The present data therefore provide initial evidence in particular to the theoretical
559 suggestions that participants implementing the SD strategy stop fast and unselectively in
560 selective SSTs and that the selective stopping process in participants implementing the DD
561 strategy might entail an additional discrimination stage.

562 Verbruggen and Logan (2015) suggest a capacity sharing account that may account for RT
563 patterns in selective SSTs without assuming different strategies for task completion. They
564 propose that in selective SSTs dependency between going and stopping may arise since the
565 decision to stop or not will share processing capacity with the go process in terms of dual
566 task interference. Of note, Bissett and Logan (2014) also suggested that dual task
567 interference may underlie the dependence of going and stopping in DD. According to
568 Verbruggen and Logan (2015), the dependency of go and stop processes will be strong in
569 particular when the decision whether or not to stop is difficult and thus yields high demands
570 on the rule-based system, on memory or on both. Hence, if signal discrimination is difficult
571 stop RT and ac RT should both be slower than go RT reflecting the RT pattern of the DD
572 strategy. If signal discrimination is of moderate difficulty, stop RT should be faster than go RT
573 while still some dependency of go and stop processes should be present resulting in slower
574 ac RT than go RT (Verbruggen and Logan, 2015). This reflects the RT pattern of the SD
575 strategy. Yet, if signal discrimination is very easy there should be little to no cost to resolving
576 this discrimination. In this case, stop RT should be faster than go RT and ac RT should not
577 be slower than go RT reflecting the RT pattern of the ID strategy. While the capacity sharing
578 framework bears high potential to explain RT patterns in selective SSTs without invoking
579 different strategies, it is important to note that it has been developed based on a study that
580 deviates in several important aspects from the present work as well as from work by Bissett
581 and Logan (2014) which may impede direct transmission of the framework to these studies.
582 First, Verbruggen and Logan (2015) used a selective stop change task in which participants
583 were required to stop a response and instead perform another response in case of a stop

584 signal. Furthermore, ac signals (18.75%) were presented much more frequently than stop
585 signals (6.25%). These differences in task design may result in different performance or
586 strategies than a selective SST as presently used. Of note, Bissett and Logan (2014) showed
587 that when ac signals are more frequent than stop signals, most participants use the DD
588 strategy in which stopping interacts with the go process. This is particularly of interest since
589 Verbruggen and Logan (2015) stress this dependency which was strongly present in the
590 selective stop change paradigm they used. Yet, dependency may depend, among other
591 factors, on the percentage of stop and ac trials. Future studies need to unveil the impact of
592 the proportion of stop and ac trials as well as of the difficulty of signal discrimination on
593 dependency of discrimination and stop processes in selective SSTs. Apart from that the
594 capacity sharing account can hardly account for the number of participants having used the
595 ID and DD strategy in the present study in which discrimination of the signal was simple
596 which should have produced RT patterns reflecting SD strategy. Although RT patterns
597 reflecting SD strategy were most frequently observed in the present sample, deviating RT
598 patterns would then have to rely on individual differences in capacity sharing or on individual
599 differences in task bias (i.e., prioritizing the stop of go process, cf. Verbruggen and Logan,
600 2015), and thus on different task strategies. As Verbruggen and Logan (2015) acknowledge
601 their framework does not preclude the use of task strategies. We therefore see both
602 frameworks, the quantitative capacity sharing framework by Verbruggen and Logan (2015)
603 and the rather qualitative approach of selective stopping strategies by Bissett and Logan
604 (2014), as complimentary approaches.

605 In sum, the present findings have important implications for future neuroimaging studies. Our
606 data imply that the neural network involved in outright stopping is robustly and uniformly
607 activated across all strategies. Neural networks specifically involved in outright stopping can
608 thus be isolated from those involved in attentional capture irrespective of the strategy applied
609 by means of stimulus-selective stopping tasks and fMRI. However, strategic differences must
610 be considered when assessing neural correlates of attentional capture. Brain activity in
611 individuals using the SD strategy differs significantly in prefrontal regions from both other

612 strategies and can be linked to unselective braking upon viewing critical signals. Since
613 unselective stopping in individuals applying the SD strategy is clearly reflected in
614 neuroimaging data, it is crucial to control neuroimaging data sets for the use of this strategy.

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728

Figure legends

Figure 1 Stop-signal task with attentional capture (ac) trials. Participants were instructed to press a button corresponding to the pointing direction of an arrow (go trials, 50%). In stop trials (25%), the arrow changed its color from white to blue after a variable stop-signal delay indicating that the participants should cancel the response. In ac trials (25%), the arrow changed its color from white to green after a variable ac signal delay. Participants were instructed to continue their response in ac trials. The attribution of color (green/blue) to trial type (stop/ac) was counterbalanced across participants

Figure 2 Decision matrix for strategy assignment based on go reaction time (RT), attentional capture (ac) RT and stop RT on incorrect stop trials (adapted from Bissett and Logan, 2014).

Figure 3 Correlation of behavioral measurements of attention-related processes and outright stopping with respective brain activity. Reaction time increase on attentional capture (ac) trials (ac RT – go RT) correlated negatively with right inferior frontal junction (IFJ) activity during attentional capture (left panel). Stop-signal reaction time (SSRT) correlated positively with bilateral inferior frontal gyrus (IFG)/ anterior insula during outright stopping (middle and right panel, respectively). MNI coordinates are given in brackets. Contrast estimates on x-axis in arbitrary units.

Figure 4 Comparison of brain activation during attentional processing (ac > go) in *Stop then Discriminate Strategy* (SD) and *Dependent Discriminate then Stop Strategy* (DD). The group contrast reveals increased activity in the inferior frontal junction in SD as compared to DD. The map is thresholded at p_{FWE} <0.05, cluster extent k = 5 voxel. The color bar represents *t*-scores

Figure 5 Group comparisons in prefrontal regions during a) attentional processing (ac>go) and b) outright stopping (stop>ac). Activation maps are collapsed across strategies for attentional processing (left panel) and outright stopping (right panel). All maps are thresholded at p_{FWE} <0.05, cluster extent k = 5 voxel. The color scale represents *t*-scores.

Group comparisons have been conducted for the following regions of interest: right and left inferior frontal gyrus (IFG)/anterior insula (ant. insula), right inferior frontal junction (IFJ) and pre-supplemental motor area (pre-SMA). MNI-coordinates are given in brackets. Strategy-dependent differences in prefrontal regions are present during attentional processing, whereas outright stopping results in indistinguishable brain activity patterns in all strategies. Error bars depict the standard error of the mean. Given *p*-values are Bonferroni-corrected for multiple comparisons.

762 **Table 1** Strategy specific behavioral results

	ID (N=18)		SD (N=31)		DD (N=27)	
	Mean	SD	Mean	SD	Mean	SD
RT go (ms)	487.14	98.27	489.10	107.09	435.45	123.46
RT ac (ms)	502.99	98.38	539.13	133.12	480.16	133.97
RT unsuccessful stop (ms)	423.78	83.69	431.89	88.14	417.70	106.85
SSRT [go distribution] (ms)	232.43	34.71	217.73	35.92	241.10	36.34
SSRT [ac distribution] (ms)					260.66	33.41
Stop signal delay (ms)	224.02	95.91	247.79	105.30	184.83	137.06
unsuccessful stop (%)	50.56	4.94	49.50	3.15	53.79	6.07
incorrect go (%)	0.66	1.10	0.40	0.79	0.66	0.69
incorrect ac (%)	0.33	0.55	0.50	0.96	0.66	0.95
omission errors go (%)	1.13	1.33	0.69	0.89	0.98	1.65
omission errors ac (%)	2.58	4.31	2.34	4.18	2.51	4.64

763

764 Behavioral data separately for each group: ID = independent stop then discriminate strategy; SD = stop then
765 discriminate strategy; DD = dependent discriminate then stop strategy. Stop-signal reaction time (SSRT) was
766 estimated using the integration method. For SSRT [go distribution], go RT distribution was used as an estimate of
767 the underlying go distribution on stop trials. For SSRT [ac distribution], ac RT distribution was used as an estimate
768 of the underlying go distribution on stop trials (for DD only). Percentage error is estimated by dividing the number
769 of incorrect trials by the total number of the respective trial type.

770

771

772 **Table 2** Bayes factors resulting from Bayesian ANOVAs testing for differences between
773 selective stopping strategies in regions of interest.

region of interest	BF_{10}	Error (%)
Attentional capture (ac > go)		
right IFG/ anterior insula	5.513	0.015
left IFG/ anterior insula	77.550	0.010
right IFJ	15.288	0.014
pre-SMA	0.414	0.038
Outright stopping (stop > ac)		
right IFG/ anterior insula	0.138	0.026
left IFG/ anterior insula	0.207	0.030
right IFJ	0.261	0.032
pre-SMA	1.297	0.026

774 *Note*: BF = Bayes factor; IFG = inferior frontal gyrus; IFJ = inferior frontal junction; pre-SMA = pre-
775 supplemental motor area.