Behavioral/Cognitive

Neural Architecture of Selective Stopping Strategies: Distinct Brain Activity Patterns Are Associated with Attentional Capture But Not with Outright Stopping

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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 the following 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 that 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, regardless 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.

Key words: **functional magnetic resonance imaging; inferior frontal gyrus; inferior frontal junction; response inhibition; stop-signal task**

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 behavioral 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 the neural underpinnings of response inhibition from those of attentional capture (ac) 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 (SSTs) have been instrumental in dissociating the neural underpinnings of attentional capture and response inhibition (Aron et al., 2007; Sharp et al., 2010; Boehler et al.,

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2011; Cai and Leung, 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 ac signals, which are matched to stop signals regarding 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 the disentangling of the 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 (ID) strategy]. However, participants using the stop then discriminate (STD) strategy unselectively inhibit their response upon the 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 trials but also on ac trials. In the third strategy, the dependent discriminate then stop (DD) strategy, the requirement to discriminate stop and ac signals interacts with the go process, thereby slowing the 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 an SST (for discussion, see Bissett and Logan, 2014).

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, can selective SSTs be used to separate stopping and attention-related neural activity. The theoretical notions of Bissett and Logan (2014) imply that while in the ID strategy inhibitory and attention-related processes are fully independent, in the STD strategy 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 the STD strategy in the sense of subtracting at least some neural activation involved in stopping. Similarly, the dissociation of inhibitory and attentional networks in the DD strategy 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 of 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 the ID strategy. The STD strategy was hypothesized to be associated with enhanced right IFG activity during ac and attenuated right IFG activity during stopping. The DD strategy was expected to show altered network activity due to the interaction of discrimination and go processes.

Materials and Methods

Participants

In total, 87 healthy humans 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 before 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 been published previously (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 used 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 before the scanning session. All participants accomplished three runs of the selective SST during the scanning session.

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. Before the beginning of each run, instructions were given orally. Instructions equally stressed the speed and accuracy of responding.

The task comprised the following 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 500 ms. Then a white arrow was displayed for 1000 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 stops per run. The initial SSD was set to 210 ms. If the response was not successfully inhibited (commission error), the SSD in the next stop trial was decreased by 30 ms with a minimum SSD of 40 ms. If a response was successfully inhibited (successful

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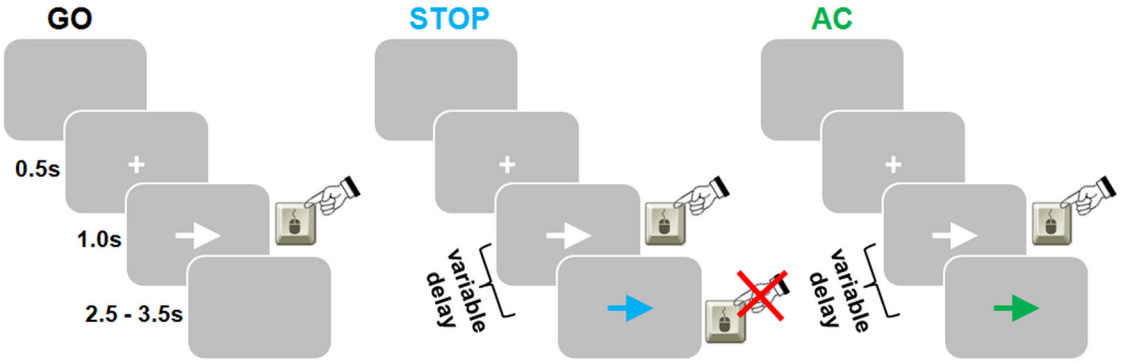

Figure 1. Stop-signal task with ac trials. Participants were instructed to press a button corresponding to the pointing direction of an arrow (go trials, 50%). In stop trials (25%), the arrow changed its color from white to blue after a variable stop-signal delay indicating that the participants should 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.

stop), the SSD in the next stop trial was increased by 30 ms. 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 500 ms) to maintain the participants' attention and to limit proactive slowing. The length of the intertrial interval was varied randomly between 2500 and 3500 ms. The presentation of fixation cross, arrow, and intertrial interval added up to an average trial duration of 4500 ms. 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 version 23 (IBM). Measures of interest were the mean RT on correct go and correct ac trials as well as on unsuccessful stop trials, and the 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 the DD strategy, 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 taken only 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 STD strategies because for these strategies context independence is given. Given these preconditions, comparisons of SSRT between the DD and both other strategies should be interpreted with caution and should be viewed as a first approximation.

Stimulus-selective stopping strategies. The following three selective stopping strategies were defined following Bissett and Logan (2014) (Fig. 2, decision matrix that was used for strategy assignment of each participant). (1) ID strategy: 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 than the 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 with go trials. (2) STD strategy: 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, the RT in ac trials should be longer than in go trials, whereas the RT in unsuccessful stop trials should be faster compared with go trials due to assumed context independence. (3) DD strategy: the requirement to discriminate stop and ac signals may interact with the go process. The RT will consequently be slowed down whenever a critical signal is detected, resulting in RT in unsuccessful stop trials, which are not shorter than the go RT, whereas the RT in ac trials should be longer than in go trials. The dependency violates the assumptions of the independent race model.

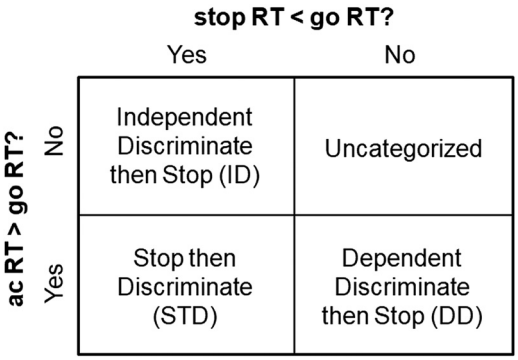

Figure 2. Decision matrix for strategy assignment based on go RT, ac RT, and stop RT on incorrect stop trials (adapted from Bissett and Logan, 2014).

To classify each participant, we followed the procedure described by Bissett and Logan (2014). In short, the mean RT for go, ac, and unsuccessful stop trials was compared for each participant, and the implicated strategy was assigned. To compare the evidence for and against the null hypotheses without bias, the Bayes factor (BF), 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 >1 support the null hypothesis, whereas numbers <1 support the alternative hypothesis. In accordance with Bissett and Logan (2014), we therefore accepted the null hypothesis when the Bayes factor was >1 and accepted the alternative hypothesis when the Bayes factor was <1. In comparing the stop RT and the go RT, we accepted the alternative hypothesis only if the stop RT was faster than the go RT. The Bayes factor was determined by calculating the mean and SD of the go RT, ac RT, and unsuccessful stop RT separately for each participant.

Then, the go RT and the unsuccessful stop RT as well as the 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 Laboratory website (http://pcl.missouri.edu/bf-two-sample) with the recommended Jeffrey-Zellner-Slow Prior with a 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) 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 dataset was obtained using a 3D magnetization-prepared rapid acquisition gradient echo sequence for registration purposes (site 1: TR = 2250 ms, TE = 2.6 ms, flip angle = 9°, FOV = 256 mm, 176 sagittal slices, voxel size = $1 \times 1 \times 1$ mm^3; site 2: TR = 1900 ms, TE = 2.52 ms, flip angle = 9°, FOV = 256 mm, 176 sagittal slices, voxel size = $1 \times 1 \times 1$ mm^3). fMRI images were obtained using T2*-weighted echoplanar imaging sequence (both sites: TR = 2500 ms, TE = 30 ms, flip angle = 90°, FOV = 192 mm, 36 slices, voxel size = $3 \times 3 \times 3$ 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 (MathWorks). Images were screened for motion artifacts before 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 6 df rigid body transformation. The realigned functional images were coregistered 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 (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) 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 cutoff period of 128 s to remove drifts or other low-frequency artifacts in the time series. After convolution with a canonical hemodynamic response function, the following 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 the neural activation patterns of the three groups (i.e., ID, STD, and DD groups) 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 full-factorial models with group (ID, STD, and DD strategies) as the between-subject factor. The 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 [familywise 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. 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 (SMA), and right IFJ; Levy and Wagner, 2011; Swick et al., 2011; Sebastian et al., 2013; Cai et al., 2014]. Since ROI analyses should be performed only in truly active regions (Kriegeskorte et al., 2009), we used a *t*-contrast thresholded at $p_{FWE} < 0.001$ that tested the average of stopping and attentional capture against simple going (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 ($x = 42$, $y = 10$, $z = 42$). rfxplot (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 ANOVAs of the extracted contrast estimates were used for statistical assessment with group (ID, STD, and DD strategies) as the between-subject factor. In addition to the classical ANOVAs, we computed Bayesian ANOVAs (Rouder et al., 2012, 2016, 2017; Wetzels et al., 2012) using JASP version 0.8.1.2 (JASP Team, 2017; 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})] (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).

Table 1. Strategy-specific behavioral results

	ID strategy ($N = 18$)		STD strategy ($N = 31$)		DD strategy ($N = 27$)	
	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

The stop-signal reaction time (SSRT) was estimated using the integration method. For SSRT [go distribution], the go RT distribution was used as an estimate of the underlying go distribution on stop trials. For SSRT [ac distribution], the ac RT distribution was used as an estimate of the underlying go distribution on stop trials (for DD strategy only). The percentage error is estimated by dividing the number of incorrect trials by the total number of the respective trial type.

Results

Behavioral data

Participants performed accurately as indicated by low error rates on the go and ac trials. The 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 the between-subject factor revealed no group differences with respect to the stopping latency as measured by the SSRT, RTs (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

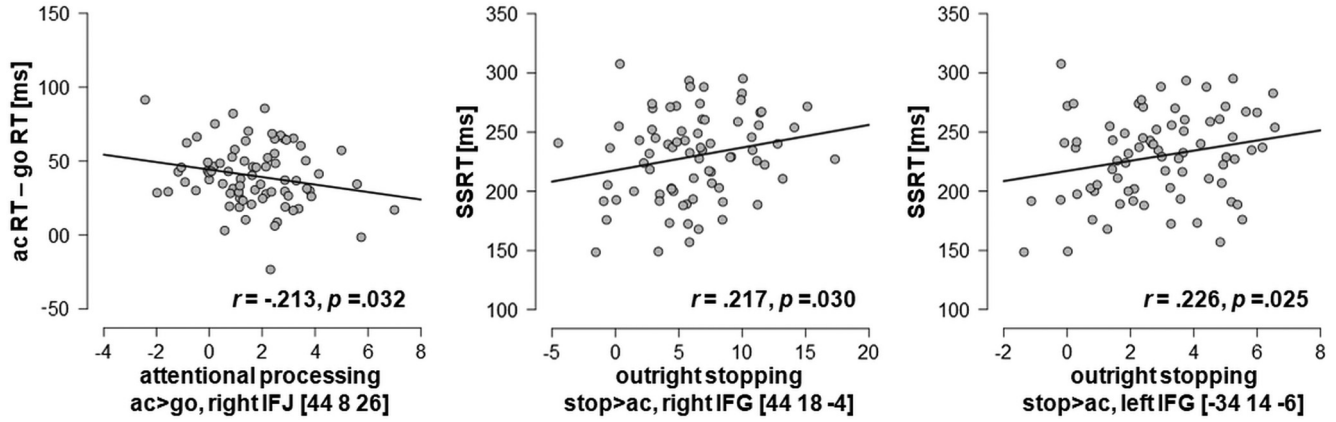

Figure 3. Correlation of behavioral measurements of attention-related processes and outright stopping with respective brain activity. Reaction time increase on ac trials (ac RT– go RT) correlated negatively with right IFJ activity during attentional capture (left). Stop-signal reaction time (SSRT) correlated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

(Bissett and Logan, 2014). Eighteen participants were assigned to the ID strategy, 31 participants used the STD 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.

We compared the SSRTs 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 a between-subject factor resulted in a significant main effect of group on SSRT based on go RT as the underlying RT distribution ($F_{(2,73)} = 3.15$, $p = 0.049$, $\eta^2 = 0.080$, $BF_{10} = 1.37$). Bonferroni-corrected *post hoc* comparisons revealed that the SSRT was slower in the DD group compared with the STD group ($p = 0.046$), while the SSRT did not significantly differ between ID and DD strategies ($p = 1.00$) or between ID and STD strategies ($p = 0.510$). When the 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 STD since independence assumptions between the stop and go processes were preserved for ID and STD, a one-way ANOVA with group as a between-subject factor again resulted in a significant main effect of group on SSRT ($F_{(2,73)} = 11.16$, $p < 0.001$, $\eta^2 = 0.234$, $BF_{10} = 9.86$). Bonferroni-corrected *post hoc* comparisons revealed that the SSRT was slower in the DD group compared with the STD group ($p < 0.001$) and was slower in the DD group compared with the ID group ($p = 0.028$).

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 dataset, 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 5 mm 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 $r = -0.213$, $p = 0.032$, one-sided test) and positive correlation of SSRT with bilateral IFG/anterior insula activity (right: Pearson's $r = 0.217$, $p = 0.030$; left: Pearson's $r = 0.226$, $p = 0.025$; one-sided test; Fig. 3). These correlations indicate that IFJ and IFG/anterior insula are involved in attentional capture and the implementation of stopping in the present sample. Brain activity within these regions can thus be viewed as markers of attention-related versus inhibitory processes to the actual behavior in the present dataset.

To compare the neural underpinnings of attentional capture and outright stopping for the three selective stopping strategies, we first performed 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 one-way ANOVAs with group (ID, STD, and DD strategies) as the between-subject 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 STD compared with DD ($x = 38$, $y = 14$, $z = 40$, $z = 5.04$; $p_{FWE} = 0.008$; Fig. 4). All other whole-brain comparisons of selective stopping strategies during attentional capture revealed no significant group differences.

The more sensitive ROI analysis resulted in significant effects during attentional capture for right IFG/anterior insula ($F_{(2,73)} = 4.99$, $p = 0.009$, $\eta^2 = 0.120$), left IFG/anterior insula ($F_{(2,73)} = 8.60$, $p < 0.001$, $\eta^2 = 0.191$), and right IFJ ($F_{(2,73)} = 6.36$, $p = 0.003$, $\eta^2 = 0.148$), whereas the ROI analysis for pre-SMA was nonsignificant ($F_{(2,73)} = 1.69$, $p = 0.192$, $\eta^2 = 0.044$). Bonferroni-corrected *post hoc t*-tests revealed that the STD group compared with the DD group displayed significantly enhanced activity within bilateral IFG/anterior insula (right, $p = 0.008$; left, $p < 0.001$) as well as in right IFJ ($p = 0.002$). In addition, the STD

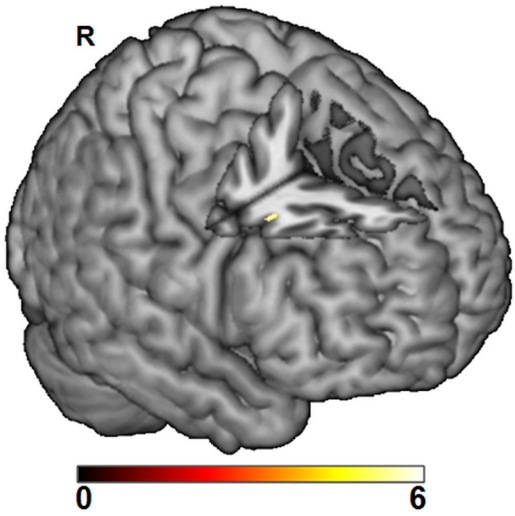

Figure 4. Comparison of brain activation during attentional processing (ac > go) in the STD and DD strategies. The group contrast reveals increased activity in the inferior frontal junction in STD strategy compared with the DD strategy. The map is thresholded at $p_{FWE} < 0.05$, cluster extent $k = 5$ voxels. The color bar represents *t* scores.

Table 2. Bayes factors resulting from Bayesian ANOVAs testing for differences between 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

BF = Bayes factor; IFG = inferior frontal gyrus; IFJ = inferior frontal junction; pre-SMA = pre-supplemental motor area.

group compared with the ID group displayed significantly enhanced activity in right IFG/anterior insula ($p = 0.048$). 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 were 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 Figure 5*a*.

Outright stopping depending on selective stopping strategies

Neither direct comparisons of selective stopping strategies nor ROI analyses (Fig. 5*b*) revealed significant group differences during outright stopping (stop > ac). More specifically, the nonsignificant results of the ANOVAs were as follows: right IFG/anterior insula ($F_{(2,73)} = 0.22$, $p = 0.806$, $\eta^2 = 0.006$); left IFG/anterior insula ($F_{(2,73)} = 0.74$, $p = 0.480$, $\eta^2 = 0.020$); right IFJ ($F_{(2,73)} = 1.05$, $p = 0.355$, $\eta^2 = 0.028$); and pre-SMA ($F_{(2,73)} = 3.09$, $p = 0.051$, $\eta^2 = 0.078$). 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 four to seven times more likely to occur under the null hypothesis than under the alternative hypothesis. For pre-SMA, the Bayes factor provided only anecdotal evidence that the data occurred more likely under the alternative hypothesis (Bayes factors are given in Table 2).

Discussion

We used direct group comparisons and 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 STD 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, 2016; Dambacher et al., 2014). 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 STD 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 STD strategy. In addition, attentional capture in STD was associated with increased IFJ activity compared with 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 STD strategy need to reinitiate 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 STD (Bissett and Logan, 2014), which is likely reflected in a frontoparietal network including IFJ (Sebastian et al., 2016). As a consequence, it is plausible that right IFJ responds stronger in STD 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 STD only after the estimated SSRT and thus after the stopping process was completed, whereas in the DD group P3 differences were observed before the estimated SSRT, hence during the stopping process. The authors suggest that the absence of neurophysiological differences between the stop and ac conditions before completion of the stopping process in the STD group support the theoretical notion of unselective stopping. In addition, P3 differences between stop and ac conditions after the completion of the stop process in the STD group might reflect differences in postprocessing steps including the reinitiation 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

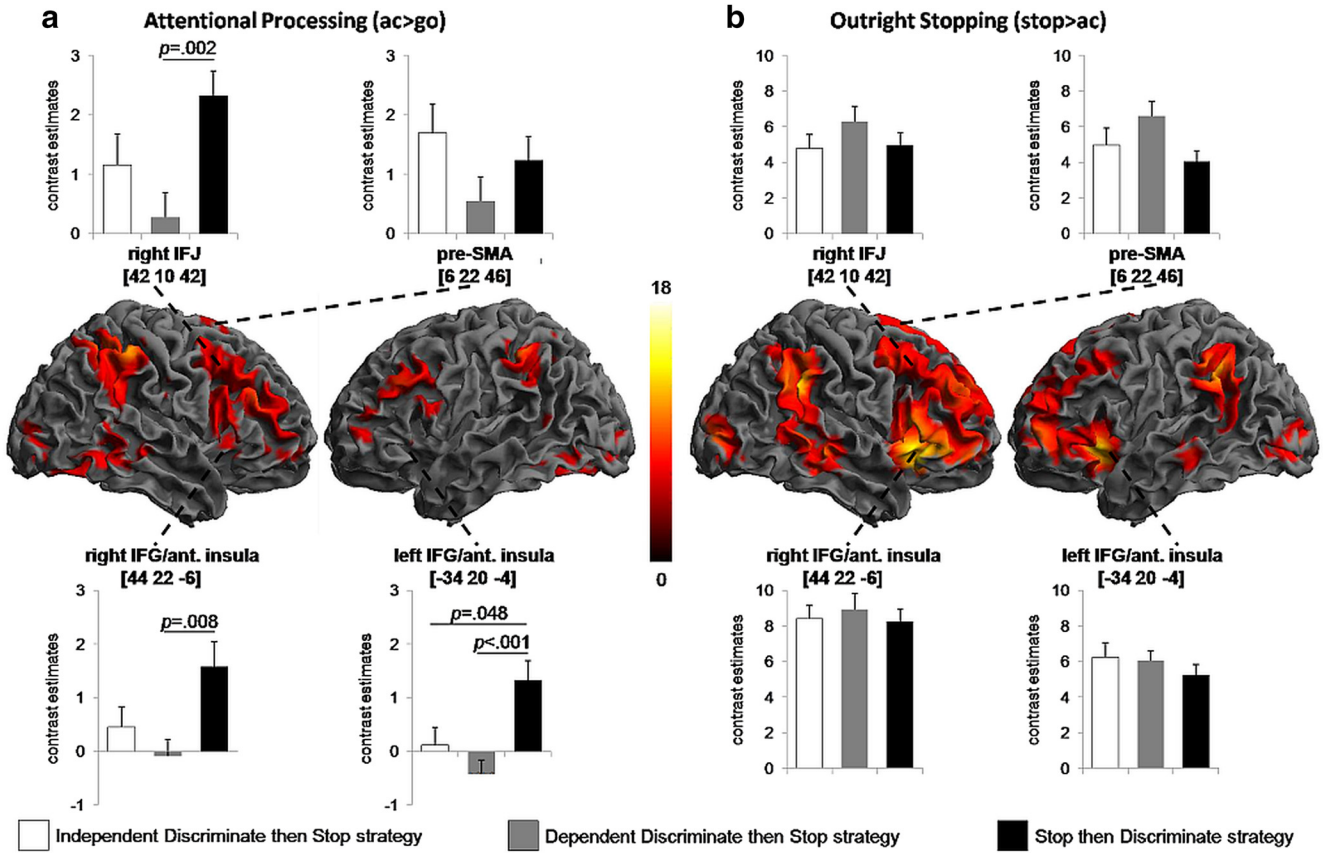

Figure 5. Group comparisons in prefrontal regions during attentional processing (ac > go; ***a***) and outright stopping (stop > ac; ***b***). Activation maps are collapsed across strategies for attentional processing (left) and outright stopping (right). All maps are thresholded at $p_{FWE} < 0.05$ (cluster extent, $k = 5$ voxels). 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 SEM. The given *p* values are Bonferroni corrected for multiple comparisons.

activity during attentional capture in the STD group. 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 the STD group and thus provide direct evidence for unselective stopping specifically in the STD group. Taken together, findings from different imaging modalities demonstrate that, in line with the theoretical notion of unselective stopping in the STD group, individuals applying this strategy also recruit the neural network involved in response inhibition on ac trials and rely on additional attention-related processes accompanied by enhanced IFJ activity to restart the go process, whereas activation patterns in the ID and DD groups support the notion of selective stopping using those strategies.

Strikingly, for outright stopping significant group differences were observed neither 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 ~0.14 and 0.26 for bilateral IFG/anterior insula and right IFJ, suggesting that these data are four to seven times more likely to be observed under the null hypothesis than under the alternative hypothesis. There was only inconclusive evidence for differences in pre-SMA activity between selective stopping strategies. The classical ANOVA for the pre-SMA just failed to reach significance, and the Bayes factors ($BF_{10} = 1.30$) were rather indecisive (note that a Bayes factor of 1 may be interpreted as no evidence and Bayes factors of 1–3 may be interpreted as anecdotal evidence; Jeffreys, 1961; Wagenmakers et al., 2017). Given the present data, evidence for differences in pre-SMA activity may thus be viewed as rather weak. Most surprisingly, the STD strategy was not associated with attenuated right IFG/anterior insula activation during outright stopping compared with the ID and DD strategies. In line with the findings of Bissett and Logan (2014), we expected individuals using the STD strategy to stop unselectively upon any critical signal before discriminating it as an ac or stop signal. Accordingly, we had hypothesized that the STD group would show activation in networks underlying response inhibition upon viewing stop as well as ac signals, which in turn should result in reduced brain activity in ventrolateral prefrontal regions when contrasting stop and ac trials compared with both other strategies. However, despite the fact that attentional capture in STD was clearly associated with brain activation of regions critically involved in response inhibition, brain activation patterns in the STD group did not significantly differ from both other strategies during outright stopping (Fig. 5*b*). This suggests that stopping upon detecting critical signals in the STD group is rather consistent with a hesitation or shortly braking than a complete stop. This fits well with the notion that the right inferior frontal cortex implements a brake that may represent a partial form of stopping (Aron et al., 2014, 2015; Wessel and Aron, 2014, 2017), probably facilitating subsequent stopping, whereas activation of the stopping network during outright stopping follows an "all-or-nothing-principle", which is uniform across all strategies.

In light of the previous literature, the present results thus suggest that participants using the STD strategy partially stop upon detecting critical signals in selective stopping paradigms. Only if the signal is identified as a stop signal, is the stopping process completed, thereby relying on the neural network involved in stopping like participants using the ID or DD strategy.

Specifically, the involvement of ventrolateral prefrontal regions in stopping tasks was subject 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 (Duncan, 2013; Erika-Florence et al., 2014; Swick and Chatham, 2014; Hampshire and Sharp, 2015a). Yet, others ascribe a brake function to the ventrolateral prefrontal cortex (VLPFC), which may slow, pause, or completely cancel an action via frontobasal–ganglia networks (Aron et al., 2014, 2015). Sharp et al. (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 et al. (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 frontobasal–ganglia network including VLPFC is generally recruited upon detecting any surprising events to briefly interrupt action and impact cognition (Wessel and Aron, 2017). This notion corresponds to the STD 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. 5*a*). 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 the STD group 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.

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 in stopping 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 (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 among other regions correlated positively with SSRT during successful stopping. Of note, the subthalamic nucleus is part of the so-called hyperdirect 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). Together, several studies including the present one provide converging evidence that stopping difficulty might be associated with stronger recruitment of a frontobasal–ganglia network.

The three selective stopping strategies differed not only with respect to their neural activation patterns, but also regarding the SSRT. The fastest SSRT was found in the STD group, and the slowest SSRT was present in the DD group. These findings are in line with findings by Sánchez-Carmona et al. (2016) and support the suggestions of Bissett and Logan (2014) that are based on the comparison of SSRTs in selective and simple SSTs. They suggested that in the ID strategy, in which the stop process is initiated after the discrimination process, selective SSRTs should be slowed down since the discrimination process of the signal is a slower process than simple signal detection (Donders, 1969). Participants applying the STD strategy, however, do not stop selectively but unselectively upon any critical signal. As the stop process occurs before the discrimination process, selective SSRTs should not differ from simple SSRTs and should thus be faster than selective SSRTs in the ID strategy. The present results are in line with this theoretical notion. For the DD strategy, Bissett and Logan (2014) expected the SSRT to be slow since the individual engages a selective stopping mechanism involving an additional discrimination stage. The present data therefore provide initial evidence in particular to the theoretical suggestions that participants implementing the STD strategy stop fast and unselectively in selective SSTs and that the selective stopping process in participants implementing the DD strategy might entail an additional discrimination stage.

Verbruggen and Logan (2015) suggest a capacity-sharing account that may explain RT patterns in selective SSTs without assuming different strategies for task completion. They propose that in selective SSTs dependency between going and stopping may arise since the decision to stop or not will share processing capacity with the go process in terms of dual task interference. Of note, Bissett and Logan (2014) also suggested that dual-task interference may underlie the dependence of going and stopping in the DD strategy. According to Verbruggen and Logan (2015), the dependency of go and stop processes will be strong in particular when the decision about whether or not to stop is difficult and thus yields high demands on the rule-based system, on memory, or on both. Hence, if signal discrimination is difficult, stop RT and ac RT should both be slower than go RT, reflecting the RT pattern of the DD strategy. If signal discrimination is of moderate difficulty, stop RT should be faster than go RT, while some dependency of go and stop processes should still be present, resulting in slower ac RT than go RT (Verbruggen and Logan, 2015). This reflects the RT pattern of the STD strategy. Yet, if signal discrimination is very easy, there should be little to no cost to resolving this discrimination. In this case, the stop RT should be faster than the go RT and the ac RT should not be slower than the go RT, reflecting the RT pattern of the ID strategy. While the capacity-sharing framework bears high potential to explain RT patterns in selective SSTs without invoking different strategies, it is important to note that it has been developed based on a study that deviates in several important aspects from the present work

as well as from work by Bissett and Logan (2014), which may impede direct transmission of the framework to these studies. First, Verbruggen and Logan (2015) used a selective stop change task in which participants were required to stop a response and instead perform another response in the case of a stop signal. Furthermore, ac signals (18.75%) were presented much more frequently than stop signals (6.25%). These differences in task design may result in different performance or strategies than a selective SST as presently used. Of note, Bissett and Logan (2014) showed that when ac signals are more frequent than stop signals, most participants use the DD strategy, in which stopping interacts with the go process. This is of particular interest since Verbruggen and Logan (2015) stress this dependency, which was strongly present in the selective stop change paradigm they used. Yet, dependency may depend, among other factors, on the percentage of stop and ac trials. Future studies need to unveil the impact of the proportion of stop and ac trials as well as of the difficulty of signal discrimination on the dependency of discrimination and stop processes in selective SSTs. Apart from that the capacity sharing account can hardly account for the number of participants having used the ID and DD strategy in the present study. Since discrimination of the signal was simple, this should have resulted in RT patterns reflecting the STD strategy. Although RT patterns reflecting STD strategy were most frequently observed in the present sample, deviating RT patterns would then have to rely on individual differences in capacity sharing or on individual differences in task bias (i.e., prioritizing the stop of the go process; Verbruggen and Logan, 2015), and thus on different task strategies. As Verbruggen and Logan (2015) acknowledge, their framework does not preclude the use of task strategies. We therefore see both frameworks, the quantitative capacity sharing framework by Verbruggen and Logan (2015) and the rather qualitative approach of selective stopping strategies by Bissett and Logan (2014), as complimentary approaches.

In sum, the present findings have important implications for future neuroimaging studies. Our data imply that the neural network involved in outright stopping is robustly and uniformly activated across all strategies. Neural networks specifically involved in outright stopping can thus be isolated from those involved in attentional capture regardless of the strategy applied by means of stimulus-selective stopping tasks and fMRI. However, strategic differences must be considered when assessing neural correlates of attentional capture. Brain activity in individuals using the STD strategy differs significantly in prefrontal regions from both other strategies and can be linked to unselective braking upon viewing critical signals. Since unselective stopping in individuals applying the STD strategy is clearly reflected in neuroimaging data, it is crucial to control neuroimaging datasets for the use of this strategy.

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