Turning the Light Switch on Binding: Prefrontal Activity for Binding and Retrieval in Action Control

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Abstract

■ According to action control theories, responding to a stimulus leads to the binding of response and stimulus features into a common representation, that is, an event file. Repeating any component of an event file retrieves all previously bound information, leading to performance costs for partial repetitions measured in so-called binding effects. Although otherwise robust and stable, binding effects are typically completely absent in "localization tasks," in which participants localize targets with spatially compatible responses. Yet, it is possible to observe binding effects in such when location features have to be translated into response features. We hypothesized that this modulation of binding effects is reflected in task involvement of the dorsolateral pFC (DLPFC). Participants localized targets with either direct (i.e., spatially compatible key) or translated (i.e., diagonally opposite to the spatially compatible key) responses. We measured DLPFC activity with functional near-infrared spectroscopy. On the behavioral level, we observed binding effects in the translated response condition, but not in the direct response condition. Importantly, prefrontal activity was also higher in the translated mapping condition. In addition, we found some evidence for the strength of the difference in binding effects in behavioral data being correlated with the corresponding effects in prefrontal activity. This suggests that activity in the DLPFC reflects the amount of executive control needed for translating location features into responses. More generally, binding effects seem to emerge only when the task at hand involves DLPFC recruitment. ■

INTRODUCTION

Imagine sitting at your desk and grabbing a coffee mug to take a sip. Such a body movement done with an intention or anticipated goal in mind is what action control theories refer to as an "action" (Frings et al., 2020; Prinz, 1998). With this definition, an action can be drinking coffee, turning a doorknob to open the door, or even just pressing a key in a laboratory task to indicate the color of a stimulus. Several theories have been developed to investigate how the cognitive system accomplishes such actions. The theory of event coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001) and the binding and retrieval in action control framework (Beste, Münchau, & Frings, 2023; Frings et al., 2020) assume that, when executing an action, all components involved in it are written into a short episodic memory trace, that is, an event file (Hommel, 2004). Upon repetition of any of its components, this event file is retrieved, affecting performance. The resulting so-called stimulus–response (S-R) binding effects can be investigated in prime–probe sequences: Here, a participant responds to two sequentially presented targets, of which response-relevant and response-irrelevant features are orthogonally varied. Fully repeating information facilitates responding, whereas partial repetitions lead to partial repetition costs as evidenced by declines in behavioral performance (Hommel, 1998, 2004).

The processes of binding and retrieval are thought to play a role in many experimental designs that involve a sequential structure, such as task switching (Koch, Frings, & Schuch, 2018), conflict tasks (Davelaar & Stevens, 2009), priming (Henson, Eckstein, Waszak, Frings, & Horner, 2014), response inhibition (Prochnow, Eggert, Münchau, Mückschel, & Beste, 2022; Prochnow et al., 2021), and others (see Frings et al., 2020). Yet, despite this ubiquity, S-R binding effects are typically completely absent in visual detection (Schöpper, Hilchey, Lappe, & Frings, 2020; Huffman, Hilchey, & Pratt, 2018) and localization (Schöpper & Frings, 2022; Hilchey, Rajsic, Huffman, Klein, & Pratt, 2018; Huffman et al., 2018) performance. From an action control perspective (Frings et al., 2020; Hommel, 2004; Hommel et al., 2001), this absence of binding and retrieval cannot be satisfactorily explained as it is incongruent with the assumption of both processes affecting all actions. It has been argued that this absence in detection and localization procedures is because of a lack of postselective processing (e.g., Schöpper & Frings, 2022; Schöpper, Lappe, & Frings, 2022; Schöpper et al., 2020; cf. Zehetleitner, Rangelov, & Müller, 2012) and/or a lack of attention to nonspatial features in these task designs (e.g., Schöpper et al.,

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2020; Hilchey et al., 2018; Huffman et al., 2018). By referring to sequential structures underlying responding as proposed in visual search (e.g., Töllner, Rangelov, & Müller, 2012; Zehetleitner et al., 2012), Schöpper et al. (2022) argued that in localization tasks—in which typically a left/right response is given to left/right targets—the localization response can be directly executed based on identifying the target. In other words, the spatially compatible localization response (e.g., Kornblum, Hasbroucq, & Osman, 1990) can be executed based on automatic visual mechanisms (e.g., Fournier, Wiediger, & Taddese, 2015; Wiediger & Fournier, 2008). In contrast, discrimination performance—in which typically a left/right response is given to the nonspatial identity of targets, leading to reliable S-R binding effects (e.g., Schöpper et al., 2020)—involves the translation of a nonspatial feature into a (spatial) response. In turn, Schöpper et al. (2022) argued that translating the spatial location feature before responding should yield S-R binding effects, whereas executing the response directly based on the location feature should not. Thus, by having participants localize targets repeating or changing their color on a touchpad by directly pressing on them versus pressing the diagonally opposite corner, the authors exactly found the predicted pattern. Schöpper et al. (2022) conclude that a translation of (spatial) feature space into response space can lead to S-R binding even in localization performance.

The underlying idea fits with other theories and findings, such as interference by spatially incompatible compared to compatible responding (e.g., Kornblum & Lee, 1995; Kornblum, 1994; Kornblum et al., 1990), a translational mechanism from (non)spatial feature space to spatial response space (e.g., Virzi & Egeth, 1985), and sequential processing demands in visual search (e.g., Töllner et al., 2012; Müller & Krummenacher, 2006). This pattern is incongruent with theoretical assumptions of an action control perspective (Frings et al., 2020; Hommel, 2004; Hommel et al., 2001) as binding and retrieval would be expected to occur in both response mappings, yet finding a binding pattern in the translated but not the direct case might be explained by having to process the location feature more strongly when translating it into a response. This focused attention on the target (location) might then lead to an increase in binding effects (see Moeller & Frings, 2014; Memelink & Hommel, 2013); in fact, making space processing more relevant in responding might trigger retrieval (Hommel, 2007; see also "space-based response hypothesis," Hilchey, Rajsic, & Pratt, 2020).

Similar to simple detection and nontranslated location tasks, previous studies have observed that binding effects are diminished in well-practiced (i.e., mostly automated) tasks (Fournier, Richardson, & Logan, 2022). A common denominator of such tasks is that they can be executed without the need for translating an arbitrary stimulus feature into a response and thus do not require a lot of executive control. Executive control in this regard refers to an assembly of higher-order cognitive operations that allow us to adapt our behavior to new or difficult situations (Diamond, 2013). Three of the most relevant executive functions comprise working memory, executive inhibition, and cognitive flexibility. Working memory allows us to internally store, manipulate, and update task-relevant information (Baddeley, 1992; Baddeley, Logie, Bressi, Della Sala, & Spinnler, 1986), inhibition allows us to dismiss task-irrelevant information or stop inappropriate behavioral routines (Friedman & Miyake, 2004; Nigg, 2000; Dempster, 1995; Harnishfeger, 1995), and cognitive flexibility allows us to switch between multiple tasks or task aspects (Diamond, 2013). Previous research on the underlying neural processes has localized essential processing steps of all three of those functions to several prefrontal brain areas depending on the respective function including, for example, the rostral pFC, the ventrolateral pFC, the inferior frontal gyrus, and the inferior frontal junction (Zhang, Geng, & Lee, 2017; Kim, Cilles, Johnson, & Gold, 2012; Owen, McMillan, Laird, & Bullmore, 2005). A functional network that seems to be heavily involved in processing related to all three functions is the dorsolateral pFC (DLPFC; Zhang et al., 2017; Kim et al., 2012; Owen et al., 2005). Fittingly, the middle frontal gyrus, partly constituting the DLPFC, has been identified to be essential in discrimination tasks measuring binding effects (e.g., Gholamipourbarogh, Ghin, et al., 2023; Wendiggensen et al., 2022; Geissler, Frings, & Moeller, 2021; Opitz, Beste, & Stock, 2020). Most relevant to our approach here is that, in EEG studies, decomposing the signal into stimulus, central, and response clusters (using residue iteration decomposition; Ouyang, Schacht, Zhou, & Sommer, 2013; Ouyang, Herzmann, Zhou, & Sommer, 2011), it was found that the translation of stimulus features into response features (measured in the central cluster and reflected in theta band activity) constituted the key process for binding effects to occur (Beste et al., 2023, for an overview).

Taken together, previous findings suggest that binding and retrieval processes depend to some degree on task-related activation of the DLPFC that possibly reflects the translation of stimulus features into response features. Thus, if a task is both too simple and task-related activation in the DLPFC is absent (or at least heavily reduced), no binding effects might be observed in this task. However, so far, this hypothesis has not been directly tested.

The Present Study

In the current study, we wanted to test the hypothesis that absence of binding effects in direct localization tasks and presence of binding effects in translated localization tasks can be explained by differential involvement of pFC activity in these tasks. Participants responded based on the location feature of targets. Crucially, responses were direct, that is, given with keys spatially compatible with targets, or translated, that is, given with keys diagonally opposite to targets. We measured task-related neural activity with functional near-infrared spectroscopy (fNIRS). fNIRS

allows for disturbance-free measurements of cortical brain activity. It utilizes near-infrared light to measure changes in oxygenated hemoglobin (oxyHB) and deoxygenated hemoglobin (deoxyHB). Either an increase in local oxyHB or a local decline in deoxyHB can signal a rise in neural activity. Both oxyHB and deoxyHB have been demonstrated to substantially correlate with the BOLD signal of the fMRI (Cui, Bray, Bryant, Glover, & Reiss, 2011; Steinbrink et al., 2006). Replicating Schöpper et al. (2022), on a behavioral level, we expected S-R binding in the translated response condition, but not in the direct condition. This S-R binding pattern would manifest in location repetitions being impeded by color changes compared to color repetitions and/or location changes being impeded by color repetitions compared to changes—in other words, we expect partial repetition costs to emerge. Note that, in our localization task, location and response are fully confounded (e.g., Schöpper & Frings, 2022; Schöpper et al., 2022; Hilchey, Antinucci, Lamy, & Pratt, 2019): Repeating the location equals repeating the response, and changing the location equals changing the response. In turn, it becomes impossible to dissociate the location feature from the response feature. It has been found that location and color as features rarely bind together (Hilchey, Rajsic, Huffman, & Pratt, 2017; Hommel, 1998, 2007; see, however, Hilchey, Pratt, & Lamy, 2019), suggesting that our design leads to binding of color to the localization response. For ease of readability, we use location throughout; however, this resembles a response based on location.

On a neural level, we expected higher DLPFC activity during translated than during direct localization. As DLPFC activity is assumed to reflect the translation of location into response features, we expected translation-related differences in behavioral binding effects and translation-related differences in prefrontal activity to be positively correlated. Note that binding effects are the result of binding and retrieval (Frings et al., 2020); in turn, activation in the DLPFC might be because of binding, retrieval, or both.

METHODS

The experimental design was an adaption of Schöpper et al. (2022). The experiment was preregistered at aspredicted.org/76qa8.pdf.

Participants

In Schöpper et al. (2022), the binding effect only emerged in the translated condition, whereas it was fully absent in the direct condition. The difference between both effects came with an effect size of $d = 0.49$. To find this effect, we aimed for $n = 30$ participants, which under an $\alpha = .05$ (one-tailed) yields a power of $1 - \beta = 0.84$ (G*Power, Version 3.1.9.4; Faul, Erdfelder, Lang, & Buchner, 2007). In total, we ran 38 participants, yet in eight cases, the fNIRS measurements did not work (too noisy, etc.), and thus, we ran participants until we reached the desired sample size of $n = 30$ (this procedure was preregistered). All participants gave written informed consent, and the experiment complied with ethics guidelines of the University of Trier. Of the final sample (27 women, 3 men; $M_{age} = 22.23$ years, $SD_{age} = 2.49$ years, age range: 19–29 years), one participant reported an uncorrected visual impairment, but the behavioral data were inconspicuous when compared with the whole sample. All other participants reported normal or corrected-to-normal vision.

Apparatus and Materials

The experiment was programmed in PsychoPy (Peirce et al., 2019). Stimuli were displayed on a monitor with a display resolution of 1280 × 1024 pixels; from an average viewing distance of 65 cm, the screen spanned 29.31° × 23.47° of visual angle. All stimuli appeared on a black (R/G/B: 0/0/0) background. A white (R/G/B: 255/255/255) fixation cross (0.71° × 0.71°) was presented at the center. Targets were red (R/G/B: 255/0/0) and blue (R/G/B: 63/72/204) circles 1.19° in diameter. Targets could appear at the top left, top right, bottom left, or bottom right. From the fixation cross, the positions were +3.48° or −3.48° on the horizontal axis and +3.48° or −3.48° on the vertical axis. By that, targets were 6.96° apart on the horizontal and vertical planes. Participants gave responses on a QWERTZ keyboard.

Design

The experiment used a 2 (Response Condition: direct vs. translated) × 2 (Location Relation: repetition vs. change) × 2 (Color Relation: repetition vs. change) within-participant design. A binding effect is derived from the interaction of location and color; its modulation is derived from the three-way interaction.

Procedure

The procedure was adapted from previous studies (Schöpper et al., 2022; Geissler, Frings, et al., 2021; Geissler, Schneider, & Frings, 2021). Participants were tested individually in a dimly lit room. Instructions were given both verbally and on the screen. The experiment began with the instructions displayed on the screen, followed by a practice block and an experimental block for each response condition. All participants started with the translated block followed by the direct block. In a behavioral pilot study, this order yielded the strongest effects. A trial started with the fixation cross in isolation for 750 msec. In the prime display, the fixation cross was accompanied by the prime target, that is, a red or blue dot at one of the four possible locations. Participants had to indicate the location of the dot with the keys D (left middle finger), C (left index finger), M (right index finger), and K (right middle finger). In the direct condition, participants responded with the

spatially congruent keys (top left = D, bottom left = C, bottom right = M, top right = K). In the translated condition, participants responded with the keys diagonally opposite to the spatially congruent keys (top left = M, bottom left = K, bottom right = D, top right = C). The prime display remained until response. Afterward, the fixation cross remained in isolation again, for 500 msec. In the probe display, the fixation cross was accompanied by the probe target, which again showed a colored target dot at one of the four possible locations, demanding a response as described for the prime display. After the probe response, the screen turned blank for a variable interval of 1650–5850 msec, ending a trial (see Figure 1A). If an incorrect response was given, an error message appeared for 1000 msec directly after the respective response.

From prime to probe, the location could repeat with the color repeating (location repetition with color repetition [LRCR]) or changing (location repetition with color change [LRCC]), or the location could change with the color repeating (location change with color repetition [LCCR]) or changing (location change with color change [LCCC]) in both response conditions. For location changes, there were three possible change options (horizontal, diagonal, and vertical), which were equally balanced. Each response condition started with 16 practice trials followed by 288 experimental trials. The latter was composed of 72 trials for each condition. Color and locations (including location changes) were pseudorandomly balanced across participants. In the practice block, participants received feedback for correct and incorrect responses; in the experimental block, only feedback for incorrect responses was given. After every 48th trial, participants could take a self-paced break.

fNIRS Measurement

We used an eight-source, eight-detector, portable, time-multiplexed, two-wavelength NIRSport (NIRx Medical Technologies LLC) fNIRS device to record hemodynamic changes. Optodes were fixed in a standard, 10–10 NIRS-caps (NIRx Medical Technologies LLC). To ensure that the investigated areas are relevant for binding-related neural processes, the same optode positions as in Geissler, Frings, et al. (2021) were chosen. AF3, AF4, AF7, AF8, F3, F4, FC1, and FC2 were chosen as source positions, and FP1, FP2, F1, F2, F5, F6, FC3, and FC4 were used as detector positions for optimal coverage of the middle frontal gyrus. This resulted in 18 different channels, each of which recorded the middle frontal gyrus with a specificity of 22.44% or greater (Figure 1B depicts the fNIRS montage). Signals were recorded with a frequency of 7.81 Hz and digitalized with NIRStar (NIRx Medical Technologies LLC) recording software.

fNIRS Data Preprocessing and Analysis

The NIRS Brain AnalyzIR toolbox (Santosa, Zhai, Fishburn, & Huppert, 2018) was used to preprocess and subsequently analyze raw data. First, raw voltage data recorded by the detectors were transformed into light-intensity data. Light-intensity data were then used to calculate the relative concentration of oxyHB and deoxyHB via the Beer–Lambert law (Jacques, 2013). Finally, low-frequency characteristics and outliers were removed with a wavelet filter (Molavi & Dumont, 2012). Preprocessed data were subsequently entered into a two-level general linear model. The first-level analysis included nine predictors

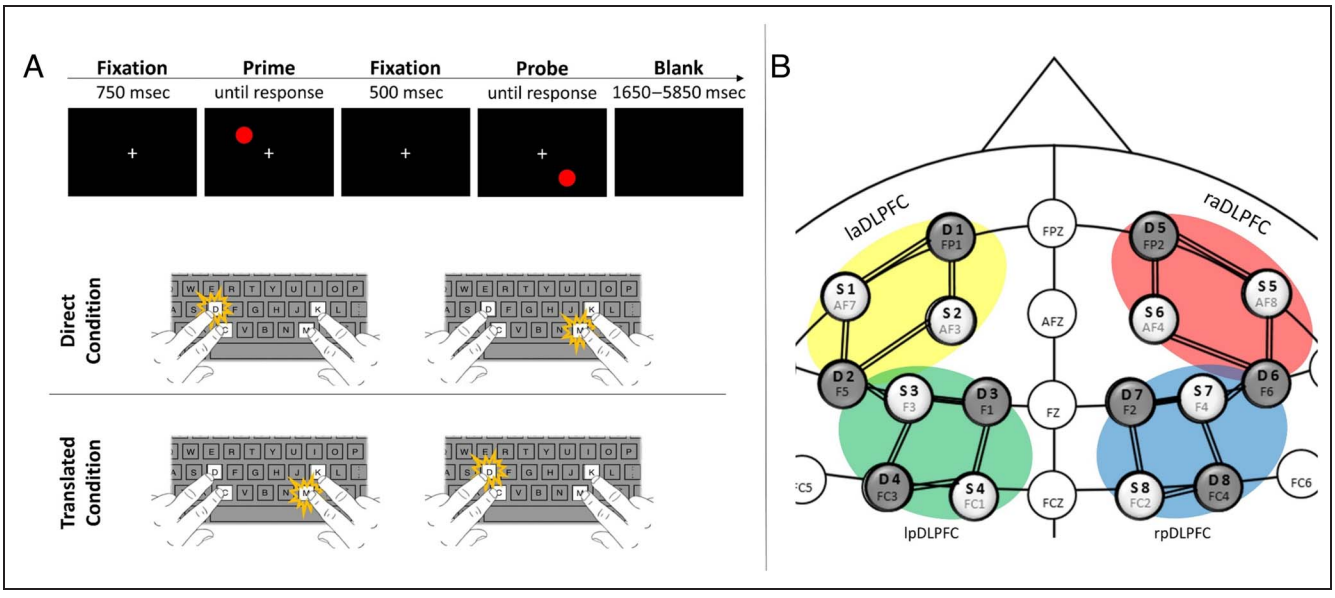

Figure 1. (A) Experimental trial sequence. Experimental sequence of an example trial (not drawn to scale), depicting a target changing its location but repeating its color (LCCR). In the direct response condition, participants had to press the spatially congruent key. In the translated response condition, participants had to press the key diagonally opposite to the spatially congruent key. (B) fNIRS montage. Light sources and detectors were placed according to the 10–10 system. To smoothen neural data, four ROIs were built. la = left anterior; lp = left parietal; rp = right parietal.

and was conducted for each participant separately. In each task type respectively, four predictors (one for each S-R binding condition) coded activity in error-free experimental trials. To account for error- and missing-related neural activity during probes (e.g., Luu, Tucker, & Makeig, 2004; Luu, Flaisch, & Tucker, 2000), an additional predictor was coded. The latter predictor was excluded from second-level analysis. General linear model predictors were generated by convolving each event with the canonical hemodynamic response function. The first and second temporal derivative of each prediction term was as well included in the model to adapt for individual differences in onset and dispersion of hemodynamic response function. An algorithm encompassing both prewhitening and robust regression (AR-IRLS; Barker, Aarabi, & Huppert, 2013) was used to correct for serially autocorrelated errors as well as artifacts induced by systemic physiology and motion. For the second-level analysis, the beta values obtained for each experimental condition for each participant were entered into a weighted mixed effects model estimating a fixed intercept for each experimental condition and a random intercept for each participant to best fit the overall data. To smoothen data, four ROIs were built as described in Santosa et al. (2018). These included the left anterior DLPFC (AF7–FP1, AF7–F5, AF3–FP1, AF3–F5), the left posterior DLPFC (F3–F5, F3–F1, F3–FC3, FC1–F1, FC1–FC3), the right anterior DLPFC (raDLPFC [AF8–FP2, AF8–F6, AF4–FP2, AF4–F6]), and the right posterior DLPFC (F4–F6, F4–F2, F4–FC4, FC2–F2, FC2–FC4; see Figure 1B). To determine activity differences between the direct and translated conditions in each ROI, activity in the four direct response conditions was subtracted from activity in the four translated response conditions. This contrast was subsequently tested against zero via a t test. To account for alpha inflation because of multiple comparisons, all p values were corrected applying positive false discovery rate (Benjamini & Hochberg, 1995). Because of the clear direction of our hypothesis, the t tests were one-sided. To test whether differences between binding effects in both conditions were correlated with differences in prefrontal activity in these conditions, participant-level betas for each blood type per ROI that showed significant differences between conditions on the group level were tested against zero via a t test. Again, this t test was one-sided. The resulting t values for each participant were then correlated with the differences in behavioral binding effects in RTs and error rates between conditions. Only contrasts and correlations that yielded corrected $p < .05$ were regarded as statistically significant.

RESULTS

RTs

Only RTs above 100 msec or below a 1.5 interquartile range above the third quartile of a participant's distribution (Tukey, 1977) were included for analysis. In addition, only trials in which the prime and probe response were both correct were included. Because of these constraints, 9.24% of probe trials were discarded.

A 2 (Response Condition: direct vs. translated) × 2 (Location Relation: repetition vs. change) × 2 (Color Relation: repetition vs. change) repeated-measures ANOVA on probe RTs (see Table 1) revealed a main effect for Response Condition, $F(1, 29) = 148.76$, $p < .001$, $\eta_p^2 = .84$, with faster responses in the direct (370 msec) compared to translated (441 msec) condition. In addition, the main effects of Location Relation, $F(1, 29) = 142.73$, $p < .001$, $\eta_p^2 = .83$, and Color Relation, $F(1, 29) = 22.50$, $p < .001$, $\eta_p^2 = .44$, were significant, with participants responding faster when repeating (358 msec) compared to changing (453 msec) the localization response and responding faster when the color repeated (403 msec) compared to changed (409 msec). The interaction between Response Condition and Location Relation was significant, $F(1, 29) = 45.00$, $p < .001$, $\eta_p^2 = .61$: In the direct condition, participants were faster when repeating (338 msec) compared to changing (402 msec) the localization response; this pattern was more strongly pronounced in the translated condition (LR: 379 msec; LC: 504 msec). The interaction of Response Condition and Color Relation was not significant, $F(1, 29) = 2.20$, $p = .149$, $\eta_p^2 = .07$. The interaction between Location Relation and Color Relation was significant, $F(1, 29) = 13.24$, $p = .001$, $\eta_p^2 = .31$ (LRCR: 352 msec; LRCC: 364 msec; LCCR: 453 msec; LCCC: 454 msec). Crucially, this pattern was further modulated by response condition, $F(1, 29) = 5.81$, $p = .023$, $\eta_p^2 = .17$, suggesting different data patterns in the translated (LRCR: 371 msec; LRCC: 387 msec; LCCR: 505 msec; LCCC: 504 msec) compared to the direct (LRCR: 334 msec; LRCC: 341 msec; LCCR: 401 msec; LCCC: 404 msec) condition.

Table 1. Mean RTs in Milliseconds and Error Rates in Percentage (in Brackets) of Probe Responses as a Function of Location Relation, Color Relation, and Response Condition

	Translated Response Condition		*Direct Response Condition*	
	Location Repetition	*Location Change*	*Location Repetition*	*Location Change*
Color repetition	371 (0.14)	505 (5.33)	334 (0.48)	401 (4.60)
Color change	387 (0.43)	504 (4.42)	341 (0.48)	404 (5.24)

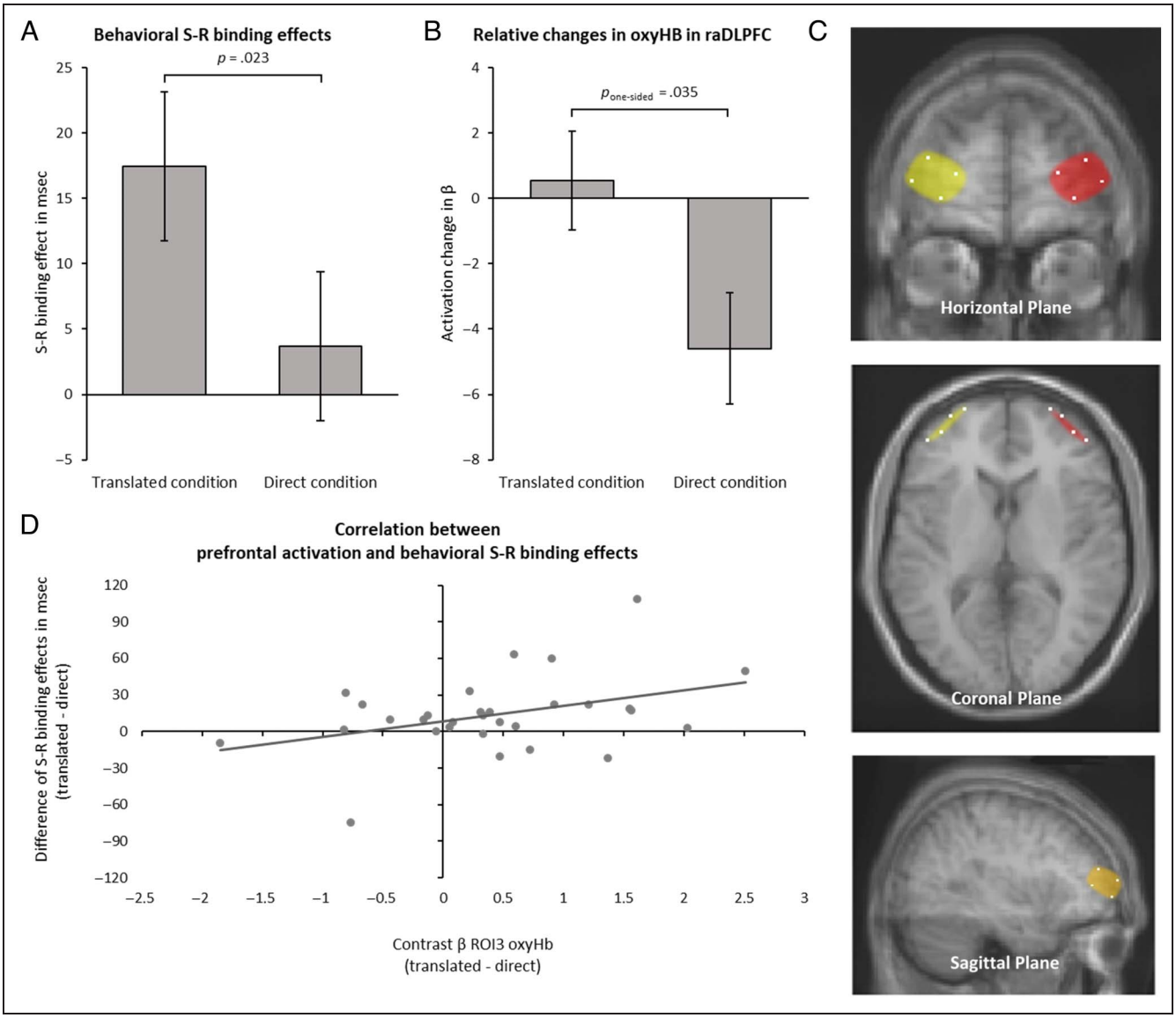

Figure 2. (A) Behavioral effects. Stimulus–response binding effects of the translated and direct conditions in RTs. Error bars represent within-participant standard error after Cousineau–Morey (Morey, 2008; Cousineau, 2005). (B) Neural effects. Relative changes in oxyHB in raDLPFC in β dependent on the translated and direct conditions. Error bars represent *SEM* with between-participant variance excluded because of including a random intercept per participant. (C) Neural effect localization. Colored areas reflect the ROIs that showed significant effects. White dots reflect the central voxel of the channels in each ROI in the horizontal, coronal, and sagittal planes. Left anterior DLPFC in yellow, raDLPFC in red, and both in orange. Colored areas are approximations only for illustration. Brain images were created with the WFU PickAtlas (3.05; Maldjian et al., 2003). (D) Correlation of behavioral and neural data.

We calculated a differential value for S-R binding as (LRCC − LRCR) − (LCCC − LCCR). This differential value sums up the partial repetition costs for (localization) response repetitions and changes (cf. Schöpper et al., 2022; Frings, 2011), that is, the cost of changing compared to repeating the color at location repetitions and the cost of repeating compared to changing the color at location changes. For the translated response condition, the differential value was 17 msec and significantly differed from zero, $t(29) = 3.58$, $p = .001$, $d = 0.65$. For the direct response condition, the differential value was 4 msec and did not significantly differ from zero, $t(29) = 1.20$, $p = .240$, $d = 0.22$. Both effects (Figure 2A) significantly differed from each other, $t(29) = 2.41$, $p = .023$, $d = 0.44$.

Error Rates

Error rates are the percentage of incorrect probe responses given after correct prime responses. In turn, all trials with incorrect prime responses were excluded from analysis, that is, 2.84%. The same ANOVA as described for RTs but now on probe error rates (see Table 1) revealed a main effect for Response Relation, $F(1, 29) = 57.56$, $p < .001$, $\eta_p^2 = .67$, with participants making less errors when repeating (0.38%) compared to

changing (4.90%) a localization response. The three-way interaction between Response Condition, Location Relation, and Color Relation approached significance, $F(1, 29) = 3.16, p = .086, \eta_p^2 = .10$ (translated condition: LRCR: 0.14%; LRCC: 0.43%; LCCR: 5.33%; LCCC: 4.42%; direct condition: LRCR: 0.48%; LRCC: 0.48%; LCCR: 4.60%; LCCC: 5.24%). None of the other effects was significant (all Fs ≤ 1.54, all ps ≥ .224). For the sake of completeness, we calculated the binding effects as described for RTs. For the translated response condition, the differential value was 1.19% and approached significance when tested against zero, $t(29) = 1.91, p = .066, d = 0.35$. For the direct response condition, the differential value was −0.64% and did not significantly differ from zero, $t(29) = -0.87, p = .392, d = -0.16$. Both effects approached significance when tested against each other, $t(29) = 1.78, p = .086, d = 0.33$.

fNIRS Results

Two ROIs showed significant differences between conditions indicating higher activity during the translated task. Thus, deoxyHB was significantly smaller during the translated than during the direct response condition in the left anterior DLPFC ($\beta = -0.6, t = -3.01, p_{\text{one-sided}} = .015$), and oxyHB was significantly higher during the translated than during the direct response condition in the raDLPFC ($\beta = 1.85, t = 2.45, p_{\text{one-sided}} = .035$). No other contrasts reached statistical significance (all other ts ≤ 1.78, all ps ≥ .107). See Table 2 for ROI-wise hemodynamic results. See Figure 2B for hemodynamic results in oxyHB in the raDLPFC.

Finally, we calculated activity differences between the translated and direct response conditions by subtracting the latter from the former. Similarly, for RTs and errors, we subtracted the differential value of the direct response condition from the differential value of the translated response condition. Thus, a higher value indicates more activity and stronger binding effects in the translated compared to direct response condition. The activity in the raDLPFC correlated significantly with the RT difference in binding effects ($r = .39, p = .034$), depicting stronger prefrontal activity yielding larger binding effects in the translated compared to direct response condition (see Figure 2C). No other correlations reached statistical significance (all ps > .846).

Table 2. Hemodynamic Results Depicting All Contrasts Between Conditions in oxyHB and deoxyHB

ROI	*HB Type*	*β (SE)*	*t*	$p_{one\text{-}sided}$
laDLPFC	oxy	0.89 (0.65)	1.38	.130
	deoxy	−0.69 (0.23)	−3.01	.015
lpDLPFC	oxy	0.95 (0.72)	1.31	.130
	deoxy	−0.19 (0.27)	−0.68	.284
raDLPFC	oxy	1.85 (0.76)	2.45	.035
	deoxy	−0.35 (0.22)	−1.59	.118
rpDLPFC	oxy	0.68 (0.38)	1.78	.107
	deoxy	−0.02 (0.17)	−0.15	.442

laDLPFC = left anterior DLPFC; lpDLPFC = left posterior DLPFC; rpDLPFC = right posterior DLPFC.

DISCUSSION

The goal of this study was to determine whether the translation of stimulus into response features (which is assumed to be a precondition for binding effects to occur; Schöpper et al., 2020, 2022) is related to DLPFC activation. We asked participants to localize targets repeating or changing their color with spatially compatible (i.e., direct) or incompatible (i.e., translated) responses while measuring prefrontal activity with fNIRS. Replicating Schöpper et al. (2022), there was an S-R binding effect in the translated but not the direct response condition. Importantly, task-related neural activation in the translated condition was significantly higher than that in the direct condition, especially in the bilateral anterior DLPFC.

These findings suggest that binding effects only occur when some stimulus features are translated into response features and further that this process is reflected in DLPFC activity. In line with this, it has been argued that theta- and alpha-band activity related to executive attentional control plays a central role in binding tasks especially for the translation of stimulus features into responses as analyzed here (Beste et al., 2023). Beyond direct visual localization, reduced need or dispensability of executive prefrontal control might be a common factor underlying several earlier findings of absent (e.g., visual detection tasks; Schöpper et al., 2020) or reduced (e.g., in overlearned tasks; Fournier et al., 2022) binding effects. It might also explain why binding effects occur in auditory spatial detection performance (Schöpper & Frings, 2023). There is evidence that human auditory spatial resolution is worse than visual spatial resolution (e.g., Loomis, Klatzky, Philbeck, & Golledge, 1998). Consequently, auditory spatial detection might constitute a need for more executive control or feature translation and thus having the potential to show binding effects. Finally, it fits well with earlier findings that responding to endogenous central arrow targets leads to binding effects, compared to an absence when responding to the position of exogenous onsets (Schöpper & Frings, 2022). Again, corroborating this, previous research has shown that endogenous but not exogenous cuing involves right DLPFC activity (Rosen et al., 1999).

The difference between task-related activation in the direct and translated conditions in the raDLPFC was also directly correlated with the difference in binding effects in these two conditions. An information-theoretical approach to pFC functioning suggests that information processing in pFC is hierarchically organized (Mansouri, Koechlin, Rosa, & Buckley, 2017; Koechlin & Summerfield,

2007; Koechlin, Ody, & Kouneiher, 2003). DLPFC processing starts in fronto-polar regions; here, states and information relevant to pending tasks are upheld, and subsequently, areas related to the DLPFC are involved in episodic control (Koechlin et al., 2003). On the one hand, this involves chunking of information (Bor, Cumming, Scott, & Owen, 2004; Bor, Duncan, Wiseman, & Owen, 2003), which functionally resembles the binding of multiple items and at least in working memory literature has been directly related to such (Oberauer & Hein, 2012; see Frings, Foerster, Moeller, Pastötter, & Pfister, in press, for a discussion of binding in action control and memory/learning). On the other hand, the DLPFC likely processes signals for guiding action selection (Koechlin & Summerfield, 2007; Courtney, 2004). This episodic control is of central relevance for event file binding processes and especially the retrieval of such because event files reflect episodic memory traces (Wendiggensen et al., 2022; Frings et al., 2020; Hommel, 2009). Given this potential involvement of the DLPFC in both binding and retrieval, the obtained correlation might signal the modulation of both binding- and retrieval-related processes. Note that the binding effect measured at the behavioral level reflects the combined effects of the strength of binding in an event file and the efficacy of retrieval processes (Frings et al., 2020), so the exact modulation—on binding and/or retrieval—is unclear.

Recently, it has been shown that there are two categories of prefrontal cortical structures during the processing of event files (Gholamipourbarogh, Prochnow, et al., 2023): Medial frontal regions seem to take a "default role" and are not modulated by the complexity of event file coding processes. In contrast, regions in the motor cortex as well as middle frontal, temporal, and superior parietal cortices are affected by the complexity modulations of event file coding processes. The current results corroborate these findings by showing that DLPFC modulations were evident when event file coding was more complex (i.e., in the translated compared to the direct response condition). It is possible that parietal cortical areas will show a similar effect as the DLPFC if measured using the experimental approach of the current study. This is not only the case because also parietal contributions to event file coding are dependent on the complexity of event file coding processes (Gholamipourbarogh, Ghin, et al., 2023; Gholamipourbarogh, Prochnow, et al., 2023). The task required a spatial transformation of stimulus feature codes into response codes. Parietal regions are central for S-R translation processes and integrate perception and action by binding sensory and motor information (Geng & Vossel, 2013; Gottlieb & Snyder, 2010; Gottlieb, 2007) and thus contribute to the selection of actions (Dilcher et al., 2021; Sulpizio et al., 2017; Cisek & Kalaska, 2005). Future studies using fNIRS should, therefore, target the role of the parietal cortex more closely for the mechanism modulated in the current study.

Of note, one has to keep in mind that the sample size that led to the correlation of behavioral and neural data was relatively low (cf. Schönbrodt & Perugini, 2013); thus, future research is needed to confirm if this is a stable link. For example, neural stimulation methods like TMS (Hallett, 2007) or transcranial alternating current stimulation (Antal & Paulus, 2013) could be employed to disrupt automated processing in a direct localization task, for example, by stimulating the extrastriate or the primary visual cortex, both of which have been linked to automated stimulus localization (Martínez et al., 2001). In theory, this disruption might trigger compensatory recruitment of higher-level areas like the DLPFC, in turn causing binding effects, even in detection or localization tasks without translation.[1]

Importantly, our study cannot pinpoint if prefrontal activation is necessary for stimulus binding, stimulus retrieval, (according to the binding and retrieval in action control framework; Frings et al., 2020) or if it simply modulates the influence of retrieved event files on action execution. This question should be tackled foremost by future research, for example, by varying task demands of succeeding responses (cf. Huffman, Hilchey, Weidler, Mills, & Pratt, 2020) or by investigating the prefrontal correlates of direct versus translated localization with EEG, which has a higher temporal resolution that allows to disentangle binding- and retrieval-related activity (Mückschel, Dippel, & Beste, 2017).

On a final note, our results might at first glance be at odds with findings of Dobbins, Schnyer, Verfaellie, and Schacter (2004) who argued that repetition of a stimulus directly retrieves the previous response and hence less DLPFC activation was measured when stimuli repeated and retrieved responses. Albeit Dobbins et al. (2004) did not discuss this finding in terms of binding and retrieval, others later on picked up these findings and argued that S-R binding is a kind of a shortcut, providing the cognitive system directly with responses, saving resources for computing the response, that is, no executive control is needed (Henson et al., 2014). Yet, the task itself that was used in these previous studies always included discrimination responses and thus translation from S to R (for instance, in the Dobbins et al. article, participants made size judgments). Our point here is that the task itself must include some form of translation and, in turn, at least to some extent, the involvement of the DLPFC for binding effects to occur.

Conclusion

We investigated whether previously found effects of absent S-R binding effects in direct localization but present S-R binding effects in translated localization are mediated by prefrontal neutral activation. Like previous research (Schöpper et al., 2022), we found binding effects only if a stimulus had to be translated before responding. Furthermore, we found significantly higher prefrontal activation in translated than direct localization. Taking into account several previous findings of absent binding effects

in particularly easy or overlearned tasks, we argue that some amount of prefrontal executive control is necessary for binding effects to manifest.

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Data Availability Statement

The experiment was preregistered at aspredicted.org/76qa8.pdf. Data of the experiment are available at https://doi.org/10.23668/psycharchives.13196. Code for analysis is available at https://doi.org/10.23668/psycharchives.13197.

Author Contributions

Christoph Felix Geissler: Conceptualization; Data curation; Formal analysis; Visualization; Writing—Original draft; Writing—Review & editing. Lars-Michael Schöpper: Conceptualization; Data curation; Formal analysis; Funding acquisition; Visualization; Writing—Original draft; Writing—Review & editing. Anna Franziska Engesser: Investigation; Project administration; Writing—Original draft; Writing—Review & editing. Christian Beste: Writing—Original draft; Writing—Review & editing. Alexander Münchau: Writing—Original draft; Writing—Review & editing. Christian Frings: Funding acquisition; Supervision; Writing—Original draft; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

Note

1. Note that although it might seem obvious to directly increase DLPFC activity to trigger binding effects—for example, by transcranial direct current stimulation (Nitsche et al., 2008)—this approach might not necessarily lead to binding effects, because it leaves the more efficient automated processing of lower-level brain areas intact. As a consequence, the higher-level processing we argue is necessary for binding effects to occur might simply be circumvented when generating a response.

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