Title: An excitatory-inhibitory fronto-cerebellar loop resolves the Stroop effect

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Abstract

The Stroop effect is a well-known behavioral phenomenon in humans that refers to robust interference between language and color information. Although this effect has long been studied, it remains unclear when the interference occurs and how it is resolved in the brain. By manipulating the verballity of stimulus perception and response generation, here we show that the Stroop effect occurs during perception of color-word stimuli and is resolved by a cross-hemispheric, excitatory-inhibitory functional loop involving the lateral prefrontal cortex and cerebellum. Humans performed a Stroop task and a control task in which the stimulus did not contain verbal information, and made a response either vocally or manually. The resolution of Stroop interference involved the lateral prefrontal cortex in the left hemisphere and the cerebellum in the right hemisphere, independently of whether the response was made vocally or manually. In contrast, such cross-hemispheric lateralization was absent during the non-verbal control task. Moreover, the prefrontal cortex amplified cerebellar activity, whereas the cerebellum suppressed prefrontal activity, and these effects were enhanced during interference resolution. These results suggest that this fronto-cerebellar loop involving language and cognitive systems regulates goal-relevant information to resolve the interference occurring during simultaneous perception of a word and color.

Introduction

The Stroop effect is widely acknowledged as a robust and intriguing behavioral phenomenon referring to a prolonged reaction time when naming the font color of a printed word if this color differs from that represented by the word's meaning¹⁻⁴ (Fig. 1a). It is thought to be attributable to interference between language and color information, and resolution of the interference requires high cognitive control.

The Stroop effect is possibly unique to humans since it relates to language functions involved in reasoning, problem-solving, and other elaborated processing operations that characterize flexible human behavior⁵⁻¹⁰. Thus, one notable signature of the Stroop effect is that these language functions persistently interfere with color information^{2, 11-15}. Despite the importance and long history of this effect, it remains unclear when it occurs and how it is resolved.

The Stroop effect was originally reported based on vocal responses^{1, 13, 16}, which involve two stages of language processing: perception of a word stimulus and generation of a vocal response (Fig. 1a). It is well known that distinct regions of the brain are responsible for these two stages^{17, 18}. Behavioral studies have also argued that core processing of the Stroop effect involves the generation of the vocal response^{15, 19, 20}. These observations suggest that response generation and its underlying neural mechanisms play an important role in the Stroop effect. However, previous neuroimaging studies of the vocal response²¹⁻²³, manual response^{12, 14, 23-27}, and covert response^{23, 28, 29} have consistently suggested that the Stroop effect is associated with the anterior cingulate, medial prefrontal, and bilateral prefrontal cortices. Nonetheless, bilateral and medial prefrontal involvement is inconsistent with the traditional view that the human language system is predominantly implicated in the left hemisphere^{18, 30}.

While Stroop tasks induce interference of verbal information processing, cognitive interference occurs in the absence of verbal information as demonstrated by flanker tasks. In a common flanker task, verbal information is not involved in either stimulus perception or response generation³¹, whereas other flanker-type tasks use a verbal stimulus^{32, 33}. Interestingly, as is the case in Stroop tasks, the interference caused by flanker tasks involves the anterior cingulate, bilateral prefrontal and parietal cortices³²⁻³⁸. This raises a question about whether the resolution of Stroop- and flanker-type non-verbal interference shares core brain mechanisms. If this were the case, such mechanisms would play a generic role in the resolution of cognitive interference beyond the verblity of the stimulus and response²³; if not, the resolution would depend on the verblity, suggesting that language processing is specifically involved in the Stroop effect³³.

It is widely accepted that the brain regions responsible for cognitive and language functions are associative neocortical regions distributed in the cerebrum^{17, 18, 30, 39}. Increasing evidence suggests that the cerebellum also plays important roles in language and cognitive control⁴⁰⁻⁴⁹. This cerebellar involvement is associated with dorsal regions in the lateral hemispheres (crura I/II, lobules VI/VIIb)^{41, 45, 46}, and is independent of sensorimotor functions implicated in rostral and caudal ventromedial regions (lobules I-VI, VIIIa/b)^{41, 50, 51}. These cerebellar regions constitute a cortico-cerebellar loop between cerebral cortical regions in the contra-lateral hemisphere^{41, 44, 50, 51}. Importantly, damage to the dorsolateral cerebellar regions impairs language functions^{41, 45, 52}, and a classical neuroimaging study reported that language processing without vocal response involves a cerebellar region in the right hemisphere⁵². This collective evidence suggests that a cross-hemispheric cerebro-cerebellar loop is involved in cognitive and language functions.

In the current study, we examined the role of language processing in the Stroop effect by manipulating the verblity of stimulus perception and response generation involved in the interference resolution. Specifically, we conducted a set of functional MRI experiments where humans performed a Stroop or non-verbal control task using vocal or manual responses (Figs. 1b-f). The non-verbal task (Swimmy task) served as a control condition in which the stimulus did not involve language information, like typical flanker tasks. Then, we comprehensively explored language processing during interference in the Stroop and Swimmy tasks (Fig. 1f), and examined directional effective connectivity between responsible brain regions to identify task-related signal flows between the regions.

Figure 1. Experimental design to examine the role of language processing in the resolution of the Stroop effect.

a, Stroop effect. It takes longer to name the color of a colored word when the word is colored in an inconsistent color (e.g., the word “RED” in blue-color font). **b**, Stroop tasks. Participants made a judgment regarding the color (*top*) or word (*bottom*) of a colored word (Stroop task). The judgement was

indicated by the orientation of the vertex of a pentagon (up: color; down: word). The word color and colored word were inconsistent (incongruent; *left*) or consistent (congruent; *right*). **c**, Control (Swimmy) tasks. Another set of participants made a judgment regarding the orientation of the vertex of a large outline of a triangle (*top*) or of small individual (*bottom*) triangles (Swimmy task). The task dimension was indicated by the color of the triangles (orange: outline; green: individual). The orientation of the outline and individual triangles was inconsistent (incongruent; *left*) or consistent (congruent; *right*). **d**, Behavioral procedures. In both the Stroop and Swimmy tasks, four trial conditions (two levels of tasks and two levels of congruency) were presented pseudorandomly. **e**, Participants responded vocally (*left*) or manually (*right*).

Results

Behavioral tasks.

A group of human participants (N = 63) performed a Stroop task. In each trial, a colored word was presented on a gray, pentagon-shaped background, and participants were required to judge the color or word of the stimulus, depending on the orientation of the pentagon vertex (Fig. 1b). The color and word were either incongruent or congruent.

Another group of participants (N = 55) performed a Swimmy task that served as a control of the Stroop task in terms of stimulus verballity, in which the stimulus did not involve verbal information. In each trial, a set of small, individual triangles was presented on the screen to form the outline of a larger triangle (Fig. 1c). Participants judged the orientation of the outline or individual triangles (in each case based on the vertex with the smallest angle), depending on the color of the individual triangles. The orientations of the outline and individual triangles were either incongruent or congruent. We named this task the Swimmy task after an old picture book in which small fish were arranged in a pattern that resembled a large fish⁵³.

In both the Stroop and Swimmy tasks, the task procedures were matched except for the nature of the visual stimulus (Fig. 1d), and participants responded either vocally (Stroop: N = 32; Swimmy: 27) or manually (Stroop: N = 31; Swimmy: 28) (Figs. 1e/f). Thus, the current experimental design consisted of two levels of stimulus modality [verbal (Stroop), non-verbal (Swimmy)] and two levels of response modality (vocal, manual), entailing a 2 x 2 factorial design (Fig. 1f). In the vocal conditions, responses were recorded through an MRI-compatible noise-reduction microphone (Supplementary Fig. 1).

Behavioral performance.

In the Stroop task, accuracy was lower in incongruent than congruent trials in both the vocal and manual conditions [vocal: $F(1, 31) = 44.0$, $P < .001$; manual: $F(1, 30) = 48.5$, $P < .001$; Fig. 2a *left*]. In the vocal Stroop task, the interaction effect of congruency

(incongruent and congruent) and task (color and word) was also significant [$F(1, 31) = 9.0, P < .01$], but such interaction was absent in the manual condition [$F(1, 30) = 1.5, P = .23$]. Accuracy was lower in the manual than the vocal condition [$F(1, 61) = 20.0, P < .001$]. The interaction effect of response modality (vocal and manual) and congruency was significant [$F(1, 61) = 15.6, P < .001$], indicating that the interference effect was greater in the manual condition, consistent with previous behavioral studies^{15, 19, 20}.

In the Swimmy task, accuracy was lower in the incongruent than the congruent trials in both the vocal and manual conditions, similar to the Stroop task [vocal: $F(1, 26) = 18.1, P < .001$; manual: $F(1, 27) = 40.6, P < .001$; Fig. 2a *right*]. In the vocal Swimmy task, the interaction effect of congruency (incongruent and congruent) and task (outline and individual) was also significant [vocal: $F(1, 26) = 5.5, P < .05$; manual: $F(1, 27) = 20.0, P < .001$], indicating that the interference effect was greater in the outline task. There was no significant difference in accuracy between the vocal and manual conditions [$F(1, 53) = 0.45, P = .51$]. The interaction effect of response modality and congruency was not significant [$F(1, 53) = 0.17, P = .68$].

Figure 2. Behavioral results.

a, Accuracy in the Stroop (*left*) and Swimmy (*right*) tasks with vocal (*top*) and manual (*bottom*) responses. The vertical and horizontal axes indicate accuracy and conditions (task and congruency), respectively. Error bars indicate standard errors of the mean across participants. The asterisks indicate significance levels [* : $P < .05$; ** : $P < .01$; *** : $P < .001$]. **b**, Reaction times. The vertical and horizontal axes indicate reaction times and conditions, respectively. Other formats are similar to those in panel A.

In the vocal conditions, reaction times were calculated as the latency from stimulus onset to vocal response onset (Supplementary Fig. 1). In the Stroop task, reaction times were longer in the incongruent than congruent trials in both the vocal and manual conditions [vocal: $F(1, 31) = 123.5$, $P < .001$; manual: $F(1, 30) = 149.3$, $P < .001$; Fig. 2b *left*]. The interaction effect of congruency and task (color and word) was insignificant in both response modalities [vocal: $F(1, 31) = 3.6$, $P = .07$; manual: $F(1, 30) = 4.1$, $P = .05$]. Reaction times were slower in the manual than vocal conditions [$F(1, 61) = 13.3$, $P < .01$]. The interaction effect of response modality and congruency was significant [$F(1, 61) = 35.3$, $P < .001$].

In the Swimmy task, reaction times were longer in the incongruent than congruent trials in both the vocal and manual conditions, similar to the Stroop task [vocal: $F(1, 26) = 111.0$, $P < .001$; manual: $F(1, 27) = 196.4$, $P < .001$; Fig. 2b *right*]. The interaction effect of congruency and task was significant in both response modalities [vocal: $F(1, 26) = 16.8$, $P < .001$; manual: $F(1, 27) = 62.1$, $P < .001$], which is attributable to greater interference effect in the outline task. Reaction times were longer in the vocal than manual conditions [$F(1, 53) = 45.2$, $P < .001$]. The interaction effect of response modality and congruency was significant [$F(1, 53) = 14.3$, $P < .001$].

These collective behavioral results demonstrated that cognitive interference was successfully imposed during the incongruent trials in both the Stroop and Swimmy tasks using vocal and manual responses.

The Stroop effect involves cross-hemispheric cerebro-cerebellar mechanisms.

In an imaging analysis, we first explored brain regions associated with the interference effect (i.e., incongruent vs. congruent trials) during the Stroop task. A strong interference effect was observed in the lateral prefrontal cortex (LPFC), posterior parietal cortex (PPC), and occipitotemporal cortex (OTC) (Fig. 3a and Supplementary Table 1; the vocal and manual conditions are collapsed). Interestingly, these prominent activations in cortical regions were observed mainly in the left hemisphere. The cerebellum also showed a strong interference effect, specifically in the crus I/lobule VI (a dorsal and caudal region) and the crus II/lobule VIIb (a dorsal and rostral region) of the cerebellar hemisphere. Notably, this cerebellar involvement was observed mainly in the right hemisphere, which contrasts with the left lateralization in the cortical regions. Involvement of the cortical and cerebellar regions was consistently observed in the vocal and manual conditions when these were analyzed separately (Supplementary Fig. 2). The medial prefrontal cortex (mPFC) and anterior cingulate cortex (ACC) also showed interference effects, which is consistent with the fact that these regions are considered to play a key role in the resolution of the Stroop interference^{12, 16, 23, 24, 29, 54-61}. The activations look weaker compared to those in the left lateral cerebral and right cerebellar regions, however.

Prior behavioral studies have demonstrated asymmetry of interference effects in the color-naming task (i.e., Stroop effect) and word-naming task (i.e., reverse-Stroop effect)⁶²⁻⁶⁵. In particular, the interference effects were greater in the color-naming task than in the word-naming task, suggesting stronger cognitive demand to attend to color. Indeed, our behavioral analysis showed a significant interaction effect of congruency and task (color and word), which is consistent with prior behavioral studies^{15, 19, 20}. To test whether the variability in behavioral interference effects is reflected in brain activity, we explored brain regions associated with the interference effect for the color and word tasks separately. In both the color and word tasks, a strong interference effect was observed in the LPFC, PPC, and OTC, all mainly in the left hemisphere, and also in right cerebellar regions; overall, the activation maps look similar for both tasks (Supplementary Figs. 3a/b). When comparing the neural interference effect between the color and word tasks, differential activity was almost absent (Supplementary Fig. 3c). Our results suggest that the Stroop and reverse-Stroop effects involve common neural mechanisms, whereas a previous study reported differential effects in cortical regions⁶⁵.

Figure 3. The Stroop effect involves a lateralized fronto-cerebellar loop during stimulus perception. **a**, Statistical activation maps for signal increase and decrease in the contrast between incongruent and congruent trials in the Stroop task ($P < .05$, FWE-corrected across the whole brain based on non-parametric permutation tests). The vocal and manual conditions were collapsed. Maps are overlaid onto a

3D surface of the brain. Hot and cool colors indicate signal increase and decrease in the incongruent trials, respectively. Arrowheads indicate anatomical locations of major activations. IPFC: lateral prefrontal cortex; PPC: posterior parietal cortex; OTC: occipitotemporal cortex; mPFC: medial prefrontal cortex; ACC: anterior cingulate cortex. **b**, Statistical maps of brain regions showing differential Stroop-effect activation (panel a) between the left and right hemispheres. Hot and cool colors indicate greater activity in the left and right hemispheres, respectively. **c**, Task-related effective connectivity analysis between IPFC and cerebellar regions based on dynamic causal modeling. The arrow directions indicate task-related effective connectivity. The magenta and green arrows indicate positive and negative effects, respectively. ***: $P < .001$.

We then asked whether the neocortical and cerebellar regions are lateralized. To this end, we contrasted the activation maps for the interference effect between the left and right hemispheres on a voxel-by-voxel basis, and then explored the brain regions showing a differential interference effect between hemispheres⁶⁶ (Supplementary Fig. 4; see also Materials and Methods). Greater activity in the left hemisphere was observed in the IPFC, PPC, and OTC. In the cerebellum, on the other hand, the crus I/lobule VI and crus II/lobule VIIb showed greater activity in the right hemisphere (Fig. 3b). These results clearly demonstrate cross-hemispheric involvement in the neocortex and cerebellum.

Given the cross-hemispheric, lateralized cerebro-cerebellar involvement, we next asked how the cortical and cerebellar regions interacted during the resolution of Stroop interference. To address this issue, we performed an interregional effective connectivity analysis based on dynamic causal modeling (DCM), which makes it possible to examine the directionality of task-related functional connectivity based on the state-space model (see Materials and Methods)⁶⁶⁻⁷². The regions of interest (ROIs) were defined as the left IPFC and the right cerebellar regions (CER; crus I/lobule VI and crus II/lobule VIIb), all of which showed robust activation (Fig. 3a) and lateralization (Fig. 3b). Specifically, for the analysis of the vocal condition, the IPFC and CER ROIs were defined as the regions showing the interference effect in the manual condition (Supplementary Fig. 2b), and vice versa (Supplementary Fig. 2a), ensuring that the ROIs were defined independently of the tested data.

In both the incongruent and congruent trials, the connectivity was excitatory from the IPFC to the CER ($P < .001$), but inhibitory from the CER to the IPFC ($P < .001$) (Fig. 3c). Interestingly, the excitatory connectivity from the IPFC to the CER and the inhibitory connectivity from the CER to the IPFC were strengthened in the incongruent trials relative to the congruent trial ($P < .001$; Fig. 3c). When the crus I/lobule VI and crus II/lobule VIIb were analyzed separately, consistent results were obtained, suggesting that these two cerebellar regions implement homologous functions

in the Stroop effect (Supplementary Figs. 5a/b). Moreover, these connectivity results were observed in the vocal and manual conditions consistently (Supplementary Figs. 5c-h), suggesting that the functional connectivity between the IPFC and the CER was independent of response modality. On the other hand, the color task showed stronger excitatory connectivity and weaker inhibitory connectivity relative to the word task (Supplementary Fig. 6).

The Swimmy effect involves bilateral cerebro-cerebellar mechanisms.

In the Swimmy task, a strong interference effect (incongruent vs. congruent trials) was observed bilaterally in the IPFC, PPC, and OTC. In the cerebellum, the crus I/lobule VI (a dorsal and caudal region) and the crus II/lobule VIIb (a dorsal and rostral region) also showed strong bilateral interference effects (Fig. 4a and Supplementary Table 2). The involvement of these cortical and cerebellar regions was predominant in both the vocal and manual conditions when these were analyzed separately (Supplementary Fig. 7). Again, activity was not as strong in the mPFC/ACC. These results suggest that the resolution of the Swimmy effect involves bilateral cortical and cerebellar regions, independently of response modality. This response-modality-independent involvement was consistent with that observed in the Stroop task. The outline and individual tasks involved similar cortical and cerebellar regions (Supplementary Figs. 8a/b), but the interference effect differed between the two tasks in multiple cortical and cerebellar regions (Supplementary Fig. 8c), possibly reflecting greater cognitive demands in the outline task, as observed in the behavioral data.

We then explored the laterality of activity during the Swimmy interference. The inferior frontal junction (IFJ) and the primary motor cortex showed stronger activity in the left hemisphere (Fig. 4b); however, compared to the Stroop task, the lateralization was weaker across the neocortical regions (Fig. 3b). It should be noted that the IFJ region is located in the posterior bank of the precentral sulcus, and is spatially separated from the IPFC region located in the inferior frontal sulcus. In the cerebellum, there was no lateralized activity. These results suggest that relative to the Stroop effect, the Swimmy effect involves neocortical and cerebellar areas more bilaterally.

Figure 4. Non-verbal Swimmy effect involves a bilateral fronto-cerebellar loop during stimulus perception.

a, Statistical activation maps for signal increase and decrease in the contrast between incongruent and congruent trials in the Swimmy task. The vocal and manual conditions were collapsed. **b**, Statistical maps of brain regions showing differential Swimmy-effect activation (panel a) between the left and right

hemispheres. IFJ: inferior frontal junction. **c**, Effective connectivity analysis between the IPFC and cerebellar regions based on dynamic causal modeling. The dashed arrows indicate insignificant connectivity. The formats are similar to those in Fig. 3.

We next performed DCM analysis of bilateral IPFC and CER ROIs. In the incongruent trials, the connectivity was excitatory from the IPFC to the CER, and inhibitory from the CER to the IPFC (Fig. 4c) ($P < .001$). However, connectivity was weak in the congruent trials ($P_s > .07$). The excitatory connectivity from the IPFC to the CER and the inhibitory connectivity from the CER to the IPFC was greater in the incongruent trials than in the congruent trials ($P_s < .001$; Fig. 4c). Again, these results are consistently observed in both the vocal and manual conditions when the two conditions were analyzed separately (Supplementary Fig. 9). Both the excitatory and inhibitory connectivity were stronger in the outline task than in the individual task (Supplementary Fig. 10).

DCM analysis of the IPFC and CER in unilateral and cross-hemispheric ROIs also exhibited excitatory and inhibitory connectivity (Supplementary Fig. 9). This suggests that in terms of functional involvement and effective connectivity, the left and right hemispheres implement homogeneous functionality during the Swimmy task, in contrast to the Stroop task.

Fronto-cerebellar involvement is independent of response modality.

To examine whether response modality (vocal vs. manual) is critical for the interference effect, we directly compared brain activity between the vocal and manual conditions (Supplementary Fig. 11). When the incongruent and congruent trials were collapsed, the vocal condition resulted in greater brain activity in the primary auditory cortex, primary motor cortex, and cerebellar lobules V/VIIIa/VIIIb, which are implicated in vocalization. On the other hand, the manual condition led to greater activity in the primary motor cortex and somatosensory cortex, and cerebellar lobules V/VI/VIIIa/VIIIb, which are implicated in right hand movement.

Next, to test whether response modality affected the interference effect, we compared the interference effect (incongruent vs. congruent) between the vocal and manual conditions (Fig. 5). In the Stroop task, greater brain activity was observed in the primary auditory cortex in the vocal condition than in the manual condition (Fig. 5a and Supplementary Table 3). On the other hand, relative to the vocal condition, the manual condition showed greater activity in the primary motor cortex and in cerebellar lobules V/VI, which are implicated in right hand movement. As in the Stroop task, the Swimmy task resulted in greater activity in the primary motor cortex and cerebellar lobules V/VI

in the manual condition than in the vocal condition (Fig. 5b and Supplementary Table 4). These results suggest that the roles of the IPFC, PPC, OTC, and cerebellum (crus I/lobule VI and crus II/lobule VIIb) in the interference effects are independent of response modalities in both the Stroop and Swimmy tasks, and the generation of a response is not critical for resolution of the interference.

Figure 5. Response and stimulus modality effects.

a, b, Response type affects the involvement of sensory-motor regions, but not the fronto-cerebellar loop associated with interference resolution.

Statistical maps showing a differential interference effect (incongruent vs. congruent) between the vocal and manual conditions. Stroop task (**a**); Swimmy task (**b**). Hot and cool colors indicate greater interference effect in the vocal and manual conditions, respectively. **c,** The Stroop effect predominantly involves the left IPFC and right cerebellum. Statistical maps showing a differential interference effect (incongruent vs. congruent) between the Stroop and Swimmy tasks. Hot and cool colors indicate a greater interference effect in the Stroop and Swimmy tasks, respectively. Formats are similar to those in Fig. 3a.

Differential cerebro-cerebellar involvement in the Stroop and Swimmy tasks.

The observations thus far demonstrated following: 1) the interference effects were independent of response modality in both the Stroop and Swimmy tasks; 2) the Stroop and reverse-Stroop effects involved similar cross-hemispheric, lateralized, cerebro-cerebellar mechanisms; and 3) the interference effects in the outline and individual tasks in the Swimmy task involved similar bilateral cerebro-cerebellar mechanisms. To directly compare the interference effects between the Stroop task (Fig. 3a) and the Swimmy tasks (Fig. 3b), we contrasted the activation maps between the two tasks. As shown in Fig. 5c and Supplementary Table 5, in the Stroop task, the interference effect was greater in the IPFC and PPC in the left hemisphere and in the crus II in the right cerebellum. On the other hand, the Swimmy task showed a greater interference effect in the PPC in the right hemisphere. These results demonstrated that while the Stroop effect involves left lateral cortical and right cerebellar regions, the Swimmy effect involves bilateral cortical and cerebellar regions.

Cross-hemispheric cerebro-cerebellar mechanisms are absent in a large-scale meta-analysis of the Stroop effect.

Previous neuroimaging studies of the Stroop effect have reported the involvement of the mPFC/ACC, IPFC, PPC, and OTC^{12, 16, 23, 24, 26, 54-61, 65, 73}. To evaluate the current observations in reference to previous studies, we compared our results with those of a large-scale meta-analysis of the Stroop effect⁶⁰. As shown in Fig. 6a (*top*), the meta-analysis revealed broad regions of involvement in the mPFC/ACC, IPFC, PPC, and OTC. In the current study, on the other hand, the involvement was left-lateralized, but overlapped well with that in the meta-analysis. Additionally, our study showed cerebellar involvement that was absent in the meta-analysis. However, the left lateralization in the cortical regions was less pronounced in the Swimmy task (Fig. 6a *bottom*) than in the Stroop task. These comparisons suggest that in our study, the results of the Swimmy task, and not those of the Stroop task, are compatible with the findings of the meta-analysis of the Stroop effect.

To quantitatively evaluate the lateralization, we performed ROI analysis. ROIs were defined as left lateral, medial, and right lateral based on X-axis coordinates on the meta-analysis map (see Methods). Then, for each ROI, activity magnitudes for the incongruent vs. congruent trials were extracted for the Stroop and Swimmy tasks. A repeated measures ANOVA with task (Stroop and Swimmy) and region laterality (left and right) revealed a significant main effect of laterality [$F(1, 116) = 105.6, P < .001$], indicating a greater interference effect in the left hemisphere in both the Stroop and Swimmy tasks. The main effect of tasks was not significant [$F(1, 116) = 0.42, P = .52$], suggesting that task demands were comparable in the Stroop and Swimmy tasks. Most importantly, the interaction effect of task and laterality was significant [$F(1, 116) = 12.9, P < .001$], indicating that left lateralization is greater in the Stroop task than in the Swimmy task. These results were consistently observed in the vocal and manual conditions (Supplementary Fig. 12).

It is well known that the resolution of cognitive interference requires cognitive control involving the IPFC and PPC^{13, 16}. We thus performed a similar ROI analysis using a meta-analysis map of cognitive control⁶⁰. Again, the current Stroop effects overlapped well with the meta-analysis map in the left hemisphere, whereas the Swimmy effects overlapped well with the meta-analysis map in both hemispheres (Supplementary Fig. 13a). In the Stroop task, the interference effect was greater in the left lateral regions [left vs. right: vocal: $t(32) = 4.5, P < .001$; manual: $t(31) = 4.9, P < .001$], and in the Swimmy task, the interference effect was observed bilaterally, and the activity did not differ between the left and right hemispheres [left vs. right: vocal: $t(27) = 1.2, P = .22$; manual: $t(28) = 0.74, P = .47$] (Supplementary Fig. 13b). On the other hand, compared to the lateral regions, the interference effect was weaker in the medial regions [Stroop: left lateral vs. medial: vocal: $t(32) = 6.1, P < .001$; manual: $t(31) = 5.5, P < .001$; Swimmy: left lateral vs. medial: vocal: $t(27) = 5.4, P < .001$; manual: $t(28) = 3.4, P < .01$; right lateral vs. medial: vocal: $t(27) = 4.2, P < .001$; manual: $t(28) = 3.5, P < .01$]. Taken together, these results clearly demonstrate that the Stroop effect is associated with the left lateral cortical regions, while bilateral cortical regions are involved in the Swimmy effect, in which stimulus perception does not involve verbal information.

To examine the interference effect in neocortical regions more specifically, the ROIs were divided into IPFC, PPC, OTC, and mPFC/ACC regions (Supplementary Fig. 14). In the Stroop task, the interference effect was greater in the left hemisphere than the right hemisphere throughout the IPFC, PPC, and OTC [IPFC: $t(63) = 6.8, P < .001$; PPC: $t(63) = 7.9, P < .001$; OTC: $t(63) = 6.8, P < .001$]. In the Swimmy task, on the

other hand, the interference effect in the left and right hemispheres did not differ for either the LPFC or PPC [LPFC: $t(55) = 0.66$, $P = .51$; PPC: $t(55) = 1.34$, $P = .19$], whereas in the OTC, the interference effect was greater in the left hemisphere [$t(55) = 4.8$, $P < .001$]. These results suggest that left lateralization of cortical involvement in the Stroop effect (Fig. 6), but not the Swimmy effect, is derived from activity in the fronto-parietal regions.

Discussion

The current study examined the neural mechanisms underlying the Stroop effect by manipulating the verblity of the stimulus to be perceived and the response to be made. The resolution of Stroop interference involved the left lateral prefrontal cortex and right cerebellum, but the lateralized involvement was not observed in the non-verbal control task. Resolution of the interference by fronto-cerebellar processes involved excitatory signaling from the prefrontal to cerebellar regions and inhibitory signaling from the cerebellar to prefrontal regions (Fig. 7a). These findings were unrelated to the verblity of the response generation. Our results suggest that Stroop interference occurs during the perception of language and color information, and is resolved by the coordinated fronto-cerebellar loop that may regulate goal-relevant information (Fig. 7b).

Figure 7. Putative model of the Stroop/Swimmy effects.

a, A schematic illustration of cerebro-cerebellar mechanisms suggested by the current results. **b**, Schematic processing diagrams of the Stroop/Swimmy effects from stimulus presentation to response execution. Anatomical structure and functionalities of the fronto-cerebellar loop are speculated based on previous anatomical and neurophysiological evidence.

Fronto-cerebellar mechanisms involved in Stroop interference.

The neocortical and cerebellar regions are thought to constitute functional-anatomical loops, specifically involving the cerebellar and pontine nuclei and basal ganglia^{41, 44, 51}. Anatomically, the loop topology has been identified not only between sensorimotor neocortical and ventromedial cerebellar regions, but also between neocortical association regions and dorsolateral cerebellar hemispheres^{41, 44} (Fig. 7b). A transneuronal tracer study in monkeys identified a loop between the lateral prefrontal cortex and dorsal regions in the lateral cerebellar hemispheres, namely, the crura I/II and lobule VIIb⁷⁴. Interestingly, in our study, homologous regions in the human prefrontal cortex and cerebellum were found to be activated during the incongruent trials (Fig. 3a), suggesting that a fronto-cerebellar loop is involved in the resolution of Stroop interference (Fig. 7).

In relation to task behavior in humans, cortico-cerebellar functional networks have been examined in sensorimotor regions^{41, 50, 51, 75, 76}. Distinct cortical and cerebellar involvement in voluntary movements is reflected in topographical parcellation of resting-state functional connectivity between the motor cortex and cerebellum⁵⁰. Notably, the lateral prefrontal and dorsolateral cerebellar regions involved in the Stroop interference in the current study also showed strong resting-state connectivity (region 12 in ref. 50).

A classical PET study revealed that language function is associated with the left lateral frontal cortex and right cerebellum, demonstrating a contra-lateral cerebro-cerebellar involvement^{41, 52}. Neuropsychological studies also showed that damage to the right cerebellum impaired language-related functions^{45, 46, 77, 78}. Consistent with these reports, our study demonstrated that a Stroop task involving language functions also relied on cross-hemispheric, lateralized, fronto-cerebellar mechanisms.

One interesting finding regarding the directional functional connectivity observed in this study is that the cerebellum sent inhibitory signals to the prefrontal cortex, whereas the prefrontal cortex sent excitatory signals to the cerebellum, a pattern that was enhanced in the incongruent trials (Figs. 3c and 7a). In the cortico-cerebellar loop, Purkinje cells receive excitatory projections from granule cells within the cerebellar cortex, and send inhibitory projections to the deep cerebellar nuclei, which

send signals to the thalamus toward neocortical regions^{41, 44, 51} (Fig. 7b). Importantly, the inhibitory projections of the Purkinje cells constitute only one output from the cerebellar cortex. Thus, the inhibitory signals from the cerebellum to the prefrontal cortex observed in our study may reflect the functionality of the Purkinje cells within the cerebro-cerebellar loop (Fig. 7b), although strong fMRI signals in the cerebellum do not reflect Purkinje cell activity alone, and may reflect other neuronal activity of granule cells^{41, 79}. As such, the strong inhibitory signaling from the cerebellum to the prefrontal cortex may help to filter out task-irrelevant signals derived from visual information that interfered with appropriate task performance in the incongruent trials (Fig. 7b).

Comparison with meta-analysis data.

Prior neuroimaging studies of the Stroop effect used manual responses mainly and reported involvement of the bilateral and medial prefrontal regions^{12, 24, 25, 61, 65, 73}. A meta-analysis map of the Stroop effect (Yarkoni et al., 2011) was created based on relevant studies. This finding is inconsistent with left-lateralized activity in cortical regions in the current study. Importantly, this discrepancy in the Stroop task was observed not only between the meta-analysis and the current vocal condition, but also between the meta-analysis and the current manual condition. Indeed, our results showed that the left-lateralized involvement of association cortices was independent of response modality (Figs. 5 and 7). In this regard, the current study may highlight a limitation of the meta-analysis approach, specifically that a collection of indecisive results can yield an unclear conclusion, providing a reasonable lesson that meta-analyses should be performed based on decisive studies.

Differential lateralization in the Stroop and Swimmy effects.

To characterize and highlight the Stroop effect involving language processing, we developed the Swimmy task as a control task in which the stimulus does not involve language information, like typical flanker tasks³¹, but rather behavioral procedures corresponded to those in the current Stroop task. Whereas the Stroop effect showed unilateral neural involvement, the Swimmy effect showed bilateral involvement, which is consistent with prior neuroimaging studies of flanker tasks^{32, 33, 36-38}. Our results also demonstrated that the involvement was independent of response modality. Collectively, these findings indicate that lateralization is dependent on stimulus modality but not on response modality (Fig. 7). Thus, our results suggest that left-lateralized cortical involvement is attributable to the visual word stimulus used in the Stroop task, which is

consistent with classical knowledge about language processing in the human brain^{17, 18}. Additionally, right-lateralized cerebellar involvement in the Stroop effect may reflect perceptual language processing, again consistent with prior neuroimaging and neuropsychological studies^{41, 45, 52}.

Interaction between stimulus congruency and response modality.

Behaviorally, in both the Stroop and Swimmy tasks, the interference effect was greater in the manual conditions than in the vocal condition (Fig. 2), consistent with previous behavioral studies^{15, 19, 20}. Neuroimaging analyses revealed that in the manual conditions, the interference effects were stronger in the primary motor and somatosensory cortices and the motor-related cerebellar regions^{41, 50, 51} in both the Stroop and Swimmy tasks (Figs. 3 and 4). In contrast, in the vocal condition, the primary auditory cortex showed stronger interference effects. These results suggest that the differences in the behavioral interference effects between the vocal and manual conditions are reflected in the greater activity in the motor and somatosensory regions. Interestingly, the association neocortices (IPFC, PPC, OTC) did not show such differential involvement between response modalities, suggesting that these regions contribute to the resolution of cognitive-language interference in both the vocal and manual conditions (Fig. 7). Taken together, the response-modality-dependent interference effects of behavior are attributable to the involvement of the motor and sensory cortices, but not the core mechanisms of interference resolution in the association cortices.

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Author contributions

M.O., D.T., M.H., and K.J. designed the experiment and study. M.O., D.T., M.H., and K.J. collected the data. M.O., T.I., M.H., K.T., and K.J. analyzed the data. M.O., M.H., M.T., K.N., and K.J. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Methods

Participants.

Written informed consent was obtained from 118 healthy young participants. Each individual participated one of the four conditions (vocal Stroop: N = 32, age range: 18-24, 8 females; manual Stroop: N = 31, age range 18-23, 11 females; vocal Swimmy: N = 27, age range: 18-23, 7 females; manual Swimmy: N = 28, age range: 18-23, 9 males). Experimental procedures were approved by the institutional review board of Keio University and Kochi University of Technology. Participants received 2000 yen for participation. All participants were right handed, had normal color vision, and spoke Japanese as a native language, and had no history of neurological or psychiatric disorders. The study sample size was determined prior to data collection based on pilot experiments and previous relevant studies. One participant in the vocal Stroop experiments was excluded from analyses due to poor behavioral performance (i.e., low accuracy in the incongruent trials; < .60).

Outline of experimental design.

A set of participants performed a Stroop task while undergoing functional MRI (Fig. 1b). Another set of participants performed the Swimmy task, an interference task in which the stimulus did not involve verbal information (Fig. 1c). The Swimmy task served as a control condition for the Stroop task. Except for the visual stimulus, identical task procedures were used in the Stroop and Swimmy tasks (Fig. 1d). During the tasks, participants responded verbally or manually (Fig. 1e). Thus, the experiments consisted of two stimulus types (Stroop, Swimmy) and two response types (vocal, manual), entailing a 2 x 2 factorial design.

Behavioral procedures.

In the Stroop task, a colored word and a gray pentagon were simultaneously presented on the screen in each trial (Fig. 1b). The word, which was composed of Japanese syllabary characters, was placed at the center of the pentagon. The colored word and the word color were blue, red, yellow, or green. Participants were required to judge the color or word in each colored word stimulus, depending on which direction in which the pentagon vertex faced. For example, if the vertex pointed upward, participants had to specify the color in the stimulus (color task), and if the vertex pointed downward, they had to specify the word in the stimulus (word task). The color and word in the stimulus were either congruent (color and word were matched) or incongruent (color and word

were unmatched). The relationship between the vertex direction and task was counterbalanced across participants.

In contrast to the Stroop task, the stimulus set in the Swimmy task did not involve verbal information. In each trial, a set of small isosceles triangles were presented (Fig. 1c). The orientation of the vertex with the smallest angle was identical for all triangles. The arrangement of the small, individual triangles formed the outline of a larger, homothetic, isosceles triangle. The outline and individual triangles pointed up, right, down, or left. Participants were required to judge the orientation of the vertex of the individual triangles or that of the large triangle outline, depending on the color of the triangles. For example, if the color of the individual triangles was orange, they had to judge the orientation of the large triangle outline, and if the color of the individual triangles was green, they had to judge the orientation of these triangles. The orientation of the outline triangle was either incongruent or congruent with those of the individual triangles. The relationship between the task and the color of the individual triangles was counterbalanced across participants. This task was referred to as the Swimmy task based on an old picture book in which a number of small fish formed the pattern of a large fish⁵³.

Both the Stroop and Swimmy tasks consisted of two tasks (Stroop: color and word; Swimmy: outline and individual) and two congruency levels (incongruent and congruent), entailing a 2 x 2 factorial design. The four conditions were presented pseudorandomly for 2 sec followed by a 2-sec fixation period (Fig. 1d). Participants were instructed to respond as accurately and quickly as possible. Each run consisted of 48 trials, with 12 trials for each of the four conditions. All visual stimuli were presented by E-Prime (Psychology Software Tools, Sharpburg PA, USA).

Except for the visual stimulus, presentation procedures were identical between the Stroop and Swimmy tasks (Fig. 1d). Participants responded either vocally or manually (Fig. 1e). In the vocal conditions, responses were recorded using an MRI-compatible microphone (FORMRI-III, Optoacoustics, Israel). In the manual conditions, participants responded by pressing a button with their right thumb.

Training procedure.

In all four experiments (stimulus: Stroop or Swimmy; response: vocal or manual), participants practiced by performing 96 trials that were presented in two separate runs (48 trials per run). Before performing the manual Stroop task, participants received an additional training session. This additional training sought to familiarize participants with the stimulus-response relationships (e.g., red: up; green: left; yellow: down; blue:

right; Fig. 1E *bottom*). In training for the color task, a colored circle patch was presented on a pentagon, and participants pressed a button corresponding to the color. In training for the word task, a color word in black font was presented on a pentagon, and participants were required to press the button corresponding to the color word. Stimulus presentation procedures were identical to those in the Stroop task. The vertex of the pentagon was randomly oriented downward or upward, but did not indicate the task to be performed. Participants performed five runs of the training task. In the other three tasks (i.e., vocal Stroop, manual Swimmy, vocal Swimmy), training for the stimulus-response relationships was unnecessary because the relationships were straightforward.

It is important that the training for the stimulus-response relationships in the manual Stroop task did not involve Stroop effects. Thus, the practice for the congruent and incongruent trials was matched across the four experiments.

Voice recording and response analysis procedures.

Vocal responses were recorded through an MRI-compatible noise-reduction microphone. For each trial, recording was started from the trial onset and stopped at the trial offset. The recording sample rate was 22 kHz. Correct and incorrect responses were sorted manually based on the record data, and trials with completely correct vocal responses within the 2-sec response window were classified as correct trials.

Because automatic MRI-noise-reduction was insufficient to allow for detection of the onset of vocal responses, an off-line band-pass filter was applied to reduce scanner-derived noise (Supplementary Fig. 1). Then, the vocal onset was defined as the first time point the magnitude of the filtered vocal data exceeded a certain threshold, and the reaction time was defined as the latency from the start of the recording to the vocal onset. The bandwidth of the filter and the threshold were determined manually for each participant by adjustment based on visual inspection of the data and detected vocal onsets.

Behavioral analysis.

For each of the Stroop and Swimmy tasks, accuracy and reaction times were calculated for each task (color or word; outline or individual), congruency condition (incongruent or congruent), and response modality (vocal or manual). They were then compared across tasks, congruency conditions, and response modalities within the Stroop or Swimmy task.

Imaging procedure.

MRI scanning was performed using a 3-T MRI scanner (Siemens Prisma, Germany) with a 64-channel head coil. Functional images were acquired using a multi-band acceleration echo-planar imaging sequence [repetition time (TR): 743 msec; echo time (TE): 35.6 msec; flip angle (FA): 48 deg; 72 slices; slice thickness: 2 mm; in-plane resolution: 2 x 2 mm; multiband factor: 8]. One functional run lasted 192 sec with 277 volume acquisitions. The initial 10 volumes were discarded for analysis to take into account the equilibrium of longitudinal magnetization. High-resolution anatomical images were acquired using an MP-RAGE T1-weighted sequence [TR: 1900 msec; TE = 2.52 msec; FA: 9 deg; 176 slices; slice thickness: 1 mm; in-plane resolution: 1 x 1 mm²].

Image preprocessing.

MRI data were analyzed using SPM12 software (<http://fil.ion.ac.uk/spm/>). All functional images were first temporally aligned across volumes and runs, and then the anatomical image was coregistered to a mean image of the functional images. The functional images were spatially normalized to a standard MNI template with normalization parameters estimated from the anatomical image. The images were then resampled into 2-mm isotropic voxels, and spatially smoothed with a 6-mm full-width at half-maximum (FWHM) Gaussian kernel.

In order to minimize motion-derived artifacts due to vocal responses, functional images were further preprocessed by general linear model (GLM) estimations with motion parameters and MRI signal time courses (cerebrospinal fluid, white matter, and whole brain), and their derivatives and quadratics as nuisance regressors⁸⁰⁻⁸² in *fsl_regfilt* implemented in the FSL suite (<http://fmrib.ox.ac.uk/fsl/>). Then residual of the nuisance GLM was used for standard GLM estimations to extract events-related brain activity described below. The same noise reduction procedure was applied to imaging data from all the experiments, including the manual conditions.

First-level GLM.

Because each participant performed one of the four experimental conditions (vocal Stroop, manual Stroop, vocal Swimmy or manual Swimmy), the four conditions were separately subjected to first-level GLM analyses. The effects of interest were task dimension (Stroop: color and word; Swimmy: outline and individual) and congruency level (incongruent and congruent). The four trial events (2 tasks and 2 congruency levels) with correct responses were coded separately in a GLM. Error trials were also separately coded in the GLM as a nuisance effect. These trial events were time-locked

to the onset of visual stimuli and then convolved with the canonical hemodynamic response function (HRF) implemented in SPM. Then, parameters were estimated for each voxel across the whole brain.

Group-level statistics.

Maps of parameter estimates were first contrasted within individual participants. The contrast maps were collected from all participants, and were subjected to a group-level one- or two-sample t-tests based on permutation methods (5000 permutations) implemented in *randomise* in the FSL suite. Then voxel clusters were identified using a voxel-wise uncorrected threshold of $P < .001$, and the identified voxel clusters were tested for significance with a threshold of $P < .05$ corrected by the family-wise error (FWE) rate across the whole brain. This group analysis procedure was validated to appropriately control the false positive rates in a prior study⁸³. The peaks of significant clusters were identified and listed in tables. If multiple peaks were identified within 12 mm, the most statistically significant peak was kept. Statistical maps were created using Connectome Workbench (<https://www.humanconnectome.org/software/connectome-workbench>) and SUI⁷⁶ (<http://www.diedrichsenlab.org/imaging/suit.htm>).

Activity lateralization analysis.

To examine the hemispheric laterality of task-related activity, we explored brain regions showing greater activity than the contra-lateral homologous regions. For each participant, contrast maps (incongruent vs. congruent) were flipped along the X (left-right) axis and were subtracted from the original non-flipped maps on a voxel-by-voxel basis⁶⁶. Then, the group-level statistical significance was tested within the left hemisphere. Note that statistical correction was performed within one hemisphere because the subtracted maps showed sign-flipped symmetry along the X axis (Supplementary Fig. 4).

Exploration was restricted to brain regions in both hemispheres that showed the interference effect ($P < .05$ uncorrected). This masking procedure ensured that positive and negative laterality effects indicated greater interference effects in the left and right hemispheres, respectively. We applied this procedure separately to the Stroop and Swimmy tasks, with vocal and manual conditions collapsed.

Effective connectivity analysis.

DCM analysis⁷⁰ implemented in SPM12 was performed in order to examine directional functional connectivity associated with the Stroop and Swimmy effects. DCM allows us

to explore the effective connectivity among brain regions under the premise that the brain is a deterministic dynamic system that is subject to environmental inputs and that produces outputs based on the space-state model. The model constructs a nonlinear system involving intrinsic connectivity, task-induced connectivity, and extrinsic inputs. Specifically, a model of neural activity was formulated as a linear time-invariant space-state dynamic system,

$$\begin{aligned}\frac{dx(t)}{dt} &= Ax(t) + u(t)Bx(t) + u(t)C \\ &= [A + u(t)B]x(t) + u(t)C\end{aligned}\quad (\text{eq. 1}),$$

where $x(t)$ denotes the states of neural activity in k brain regions ($k \times 1$ vector) at time t , $u(t)$ denotes inputs to the system from task events at time t (scalar value), A denotes intrinsic connectivity ($k \times k$ matrix), B denotes effective connectivity ($k \times k$ matrix), and C denotes the direct influence of the task variable on neural activity (direct extrinsic input; $k \times 1$ vector). Because the time derivative of neural activity (left side in eq. 1) is modulated by $[A + u(t)B]x(t)$, the directionality of connectivity is reflected in the A and B matrices. More specifically, the rows and columns of the A and B matrices indicate the target and source of the directionality. The A , B , and C matrices involved k^2 , $k(k - 1)$, and k parameters, respectively (only non-diagonal elements are parameters for matrix B). Thus, the model involved $2k^2$ parameters in total. The unit of the connectivity is arbitrary. Next, the neural activity $x(t)$ in the model (eq. 1) was transformed as

$$y(t) = \lambda(x(t)) \quad (\text{eq. 2})$$

where λ denotes a nonlinear function providing fMRI signals from neural activity.

Then, parameters of the nonlinear system (A , B , and C) are estimated based on fMRI time series and task variables/events. The use of a high temporal resolution sequence for functional imaging (TR = 0.743 s) enabled us to collect a large number of scan frames to increase the signal-to-noise ration of the DCM analysis^{66, 68, 71}.

For the Stroop task, we defined ROIs in the left IPFC and the right cerebellum (CER; lobules V/VI and crus II/lobule VIIb) that showed 1) strong activity in the incongruent condition than in the congruent condition (Fig. 3a), and 2) cross-hemispheric lateralization (Fig. 3b). Specifically, to ensure that the ROIs were defined independently of the tested data, in the analysis of the vocal condition, the left IPFC and right CER ROIs were defined as peak coordinates showing the interference effect (i.e., incongruent vs. congruent) in the manual condition, and vice versa. For the Swimmy task, we defined IPFC and CER ROIs bilaterally, given their bilateral involvement (Figs. 4a/b). As in the Stroop task, ROIs for the vocal condition were defined based on

the manual condition, and vice versa. The ROIs were created as spheres with 6-mm radii centered at the coordinates.

We then tested whether the IPFC region sent (or received) a task-related signal toward (or from) the CER region of the target during the Stroop and Swimmy tasks. Signal time courses (1335 scanning frames) of the IPFC and CER ROIs and regressors in events of interest were extracted from first-level GLMs. The events of interest were the onsets of incongruent and congruent trials. We first separately examined task-related connectivity during the incongruent and congruent trials (relative to baseline). Then we tested whether the connectivity was modulated by task parameters. Specifically, to test whether the task-related connectivity differed between the incongruent and congruent trials, the two trials were coded as a parametrical contrast effect (incongruent: 1; congruent: -1). Likewise, similar parametric effects were examined to test manipulations of tasks [i.e., color and word tasks in the Stroop task (color: 1; word: -1); outline and individual tasks in the Swimmy task (outline: 1; individual: -1)]. The input matrix was U mean-centered.

For each trial effect, causal models were defined as those that differed in modulatory effects (i.e., matrix B) among ROIs. We were interested in strengths of effective connectivity between pairs of ROIs (e.g., IPFC and CER), rather than exploration of the model that best fits to the data. Thus, we considered all theoretically possible models. In theory, there are $2^{k(k-1)}$ models that consist of k brain regions. Connectivity matrices reflecting 1) first-order connectivity (i.e., matrix A), 2) effective changes in coupling induced by the inputs (i.e., matrix B), and 3) extrinsic inputs (i.e., matrix C) on MRI signals in ROIs were estimated for each of the models based on DCM analysis implemented in SPM12. When task-related contrast was examined, a parametric regressor (incongruent vs. congruent, color vs. word, or outline vs. individual) was used as an extrinsic effect for effective connectivity between ROIs and ROIs inputs.

In order to estimate the strength of effective connectivity, a Bayesian model reduction method⁶⁷ was used. This reduction method reduces the number of models based on model evidence (free energy) and the posterior densities of the models. Specifically, only the models with a minimal posterior density greater than zero were included. These models were then inverted to a fully connected model, and supplemented by second-level parametric empirical Bayes (PEB)⁶⁷ to apply empirical priors that remove subjects' variability from each model.

Next, the parameters of these models were estimated based on Bayesian model averaging (BMA)⁷⁰ to estimate group-level statistics. Because the current

analysis aimed to identify effective connectivity observed as an average across participants, we used a fixed-effect (FFX) estimation assuming that every participant uses the same model. This is in contrast to using a random effect (RFX) estimation assuming different participants use different models, which is often used to test group differences in effective connectivity⁶⁹. The significance of connectivity was then tested by thresholding at a posterior probability at the 95% confidence interval. We used the uncorrected threshold, because the current analysis aimed to test if connectivity between two specific brain regions was enhanced depending on task manipulation and brain activity, not to identify the model of connectivity among multiple brain regions that best fits to the imaging and behavioral data^{66, 84}.

ROI analysis.

In order to examine consistency between the current study and prior neuroimaging studies, ROI analyses were performed. Statistical maps for a meta-analysis of the Stroop effect and cognitive control were obtained from Neurosynth (<https://neurosynth.org/analyses/terms/stroop/>; [https://neurosynth.org/analyses/terms/cognitive control/](https://neurosynth.org/analyses/terms/cognitive%20control/)). The uniformity-test maps were thresholded using a statistical threshold of $P < .01$ (FWE-corrected). Then ROIs were defined as left lateral, medial, and right lateral regions in the thresholded maps based on MNI X-axis coordinates. Then, for each ROI, activity magnitudes were extracted for the contrast between incongruent and congruent trials from individual participants. The extracted activity magnitudes were then averaged across participants, and compared among ROIs, response modalities, and tasks.

A supplementary ROI analysis was performed to compare activity magnitudes in the IPFC, PPC, OTC, and mPFC/ACC regions (Supplementary Fig. 14). The left lateral, medial, and right lateral ROIs of the meta-analysis maps were further classified into IPFC, PPC, OTC, and mPFC/ACC ROIs based on anatomical locations in the meta-analysis map of cognitive control.

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Supplementary Information

Title: An excitatory-inhibitory fronto-cerebellar loop resolves the Stroop effect

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Supplementary Figures

Supplementary Figure 1. Detection of vocal onsets.

Vocal data samples for the Stroop (a) and Swimmy (b) tasks. Horizontal and vertical axes indicate time from the onset of the trial and magnitudes of the vocal signals, respectively. Recorded signals (blue) were filtered, and then when the filtered data (red) exceeded a threshold, the onsets of the vocal response (green) were identified.

Supplementary Figure 2. The Stroop effect involves common lateralized cerebral and cerebellar regions in the vocal and manual response conditions.

Statistical activation maps for a signal increase or decrease in the contrast between incongruent and congruent trials for the Stroop task are separately shown for the vocal response condition (**a**) and manual response condition (**b**). Formats are similar to those in Fig. 3a.

Supplementary Figure 3. The interference effect in the color and word tasks involve common cerebral and cerebellar regions.

Statistical activation maps for a signal increase or decrease in the contrast between incongruent and congruent trials in the Stroop task are separately shown for the color task (a) and the word task (b). c, Statistical maps showing differential brain activity the interference effect between the color and word tasks. Formats are similar to those in Fig. 3.

Supplementary Figure 4. Analysis procedure for exploration of lateralized activity.

Contrast maps were flipped along the X axis (left-right), then subtracted from the original non-flipped maps before being entered into voxel-wise group-level analyses in the left hemisphere.

Supplementary Figure 5. Task-related effective connectivity between the IPFC and cerebellar regions during the Stroop task. Connectivity with the IPFC was estimated separately for the crus I/lobule VI (a) and crus II/lobule VIIb (b). c-h, The vocal and manual response conditions were analyzed separately. C-e: Vocal response condition. f-h, Manual response condition. Connectivity between the IPFC and the two cerebellar regions (c/f), between the IPFC and crus I/lobule VI (d/g), and between the IPFC and crus II/lobule VIIb (e/h). Formats are similar to those in Fig. 3c.

Supplementary Figure 6. Task-related effective connectivity for the color and word tasks in the Stroop tasks.

a/b, Vocal response condition; **c/d**, manual response condition; **a/c**, color task; **b/d**, word task. **E**, Connectivity strength was contrasted between the color and word tasks. Formats are similar to those in Fig. 3c.

Supplementary Figure 7. The Swimmy effect involves common bilateral cerebral and cerebellar regions in the vocal and manual response conditions.

Statistical activation maps for a signal increase or decrease in the contrast between incongruent and congruent trials in the Swimmy task are shown separately for the vocal response condition (**a**) and the manual response condition (**b**). Formats are similar to those in Fig. 3.

Supplementary Figure 8. The interference effect in the outline and individual tasks involve common cerebral and cerebellar regions.

Statistical activation maps for a signal increase or decrease in the contrast between incongruent and congruent trials in the Swimmy task are shown separately for the outline task (**a**) and the individual task (**b**). **c**, Statistical maps showing differential brain activity in the interference effect between the color and word tasks. Formats are similar to those in Fig. 3.

Supplementary Figure 9. Task-related effective connectivity between the IPFC and cerebellar regions during the Swimmy task.

Connectivity with the IPFC was estimated separately for the vocal response condition (**a**) and the manual response condition (**b**). **c-f**, Connectivity was estimated between the IPFC and cerebellum in either of the right or left hemispheres. **c**, Left IPFC and right cerebellum; **d**, right IPFC and left cerebellum; **e**, left IPFC and left cerebellum; **f**, right IPFC and right cerebellum.

Supplementary Figure 10. Task-related effective connectivity during the outline and individual tasks in the Swimmy task.

a/b, Vocal response condition; **c/d**, manual response condition; **a/c**, outline task; **b/d**, individual task. **e**, Connectivity strength was contrasted between the outline and individual tasks. Formats are similar to those in Fig. 3c.

Supplementary Figure 11. Vocal and manual conditions involve distinct sensory and motor regions. Statistical activation maps for a signal increase or decrease in the contrast between vocal and manual response conditions. **a**, Stroop task; **b**, Swimmy task. The incongruent and congruent trials are collapsed. Formats are similar to those in Fig. 3.

Supplementary Figure 12. Comparisons with meta-analysis data for vocal and manual conditions.

a, Meta-analysis maps of the Stroop effect and current activation maps of interference effects (incongruent vs. congruent in the Stroop and Swimmy tasks) are overlaid on transverse sections of structural images separately for the vocal and manual conditions. Formats are similar to those in Fig. 7a.

b, Regions-of-interest analysis of the Stroop and Swimmy tasks are shown separately for the vocal and manual response conditions. Formats are similar to those in Fig. 7b.

Supplementary Figure 13. Comparisons with meta-analysis data of cognitive control.

a, Meta-analysis maps of cognitive control and current activation maps of interference effects (incongruent vs. congruent) are overlaid on transverse sections of structural images. Vocal response condition (*top*); manual response condition (*bottom*); Stroop task (*left*); Swimmy task (*right*). Formats are similar to those in Fig. 7a. **b**, Region-of-interest analysis. Stroop task (*left*); Swimmy task (*right*). For each task, activity magnitudes were calculated separately for the vocal and manual response experiments. Formats are similar to those in Fig. 7b.

Supplementary Figure 14. Lateralized cortical involvement in the Stroop effect (Fig. 7), but not the Swimmy effect, is based in the fronto-parietal regions.

Regions of interest were defined as the occipitotemporal (OT), parietal (PA), and frontal (FR) regions in the left lateral, medial, and right lateral regions based on meta-analysis maps of cognitive control. Stroop task (*left*); and Swimmy task (*right*). Formats are similar to those in Fig. 6b.

Supplementary Tables

Supplementary Table 1. Brain regions showing a significant signal increase or decrease in the contrast between incongruent and congruent trials in the Stroop task. Positive and negative z-values indicate greater signals in the incongruent and congruent trials, respectively. Coordinates are listed in MNI space. BA indicates Brodmann area and is approximate.

Area	x	y	z	z-value	BA
Frontal cortex	-50	12	32	6.74	6
	-36	14	24	6.02	44
	-42	6	54	5.99	6
	48	36	26	5.44	9
	-36	28	20	5.33	9
	-2	6	60	5.08	6
	50	46	-10	4.95	10
	4	24	42	4.70	8
	-32	-6	66	4.68	6
	24	40	-20	4.55	11
	-24	0	52	4.49	6
	44	10	44	4.49	8
	-48	42	2	4.40	46
	10	20	68	4.40	6
	-22	40	-20	4.35	11
	6	28	26	4.26	32
	8	6	68	4.03	6
	-38	50	-14	3.97	10
	48	16	14	3.52	44
	30	62	-16	3.35	10
	-50	14	0	3.33	44
	-36	42	6	3.08	46
Temporal cortex	-48	-38	46	6.50	40
	-48	-60	-12	6.38	37
	36	20	2	5.10	13
	-34	16	0	4.97	13
	-2	-26	30	4.59	23
	-4	-12	32	4.45	23
	48	-38	46	4.09	40
	-58	-50	-6	3.96	37
	56	-40	-10	3.80	21
	68	-32	-10	3.77	21
	-46	-44	-14	3.53	37
	68	-50	-6	3.26	37
	60	-56	-16	3.18	37
	56	-36	56	3.09	40
Parietal cortex	-26	-68	50	6.97	7
	-36	-56	50	6.23	39
	-28	-72	30	5.16	39
	32	-56	44	5.04	39
	-10	-70	52	4.26	7
	32	-66	62	4.03	7
	12	-68	42	3.79	7
	-32	-24	72	3.78	4

	-32	-24	58	3.51	4
Occipital cortex	-34	-86	-10	6.38	18
	30	-94	-4	6.03	18
	38	-86	-8	5.43	18
	44	-72	-10	4.23	19
Cerebellum	28	-68	-46	6.21	Lobule VIIb
	34	-64	-28	5.97	Crus I
	2	-64	-26	5.83	Vermis VI
	-32	-60	-26	5.65	Lobule VI
	0	-64	-14	5.56	Lobule V
	12	-78	-34	5.54	Crus II
	6	-78	-18	5.52	Lobule VI
	20	-66	-22	5.45	Lobule VI
	-32	-64	-46	5.39	Lobule VIIb
	-8	-80	-22	5.27	Crus I
	-18	-64	-26	4.94	Lobule VI
	0	-50	-20	4.81	Lobule I-IV
	2	-46	-6	4.80	Lobule I-IV
	-28	-76	-48	4.72	Crus II
	-44	-60	-28	4.60	Crus I
	-2	-74	-32	4.59	Crus II
	12	-62	-42	4.59	Lobule VIIb
	14	-52	-16	4.47	Lobule V
	-10	6	2	4.08	Caudate
	36	-54	-48	3.89	Lobule VIIb
	10	-54	-30	3.45	Lobule I-IV
Others	12	2	4	4.99	Thalamus
	2	-18	-16	4.18	Thalamus
	14	-4	20	4.85	Caudate
	-12	-18	2	4.11	Thalamus
	-16	-14	22	4.10	Caudate
	8	-10	0	3.84	Thalamus
Frontal cortex	4	38	-10	-6.74	11
	2	50	-4	-6.67	10
	-22	32	36	-5.88	8
	2	8	-8	-5.86	25
	28	38	38	-5.78	9
	4	20	-8	-5.63	25
	-10	34	-10	-5.47	11
	-24	42	26	-5.25	10
	12	44	20	-4.94	9
	22	24	38	-4.89	8
	4	58	40	-4.68	9
	6	-14	50	-4.63	24
	-30	30	-16	-4.55	47
	-18	60	14	-4.51	10
	34	30	-14	-4.47	47
	-10	60	38	-4.40	9
	24	22	52	-4.33	8
	4	-26	58	-4.32	6
	58	4	2	-4.26	6
	-2	32	2	-4.24	24
	-14	40	18	-4.16	32
	-16	48	48	-4.12	8
	20	28	-8	-4.02	11
	26	52	40	-3.89	9
	22	8	58	-3.77	6

Temporal cortex	-16	16	50	-3.68	6
	-22	34	56	-3.51	8
	-24	60	30	-3.49	10
	2	68	14	-3.44	10
	0	4	12	-3.41	24
	56	-4	-14	-6.34	22
	-28	-40	-14	-6.33	37
	-50	18	-26	-6.18	38
	24	-40	-12	-6.11	37
	-60	0	-6	-6.00	22
	-6	-58	16	-5.97	23
	48	-16	22	-5.91	40
	14	-50	10	-5.88	23
	-52	-8	-18	-5.86	21
	32	-32	-16	-5.57	36
	48	18	-28	-5.52	38
	2	-46	22	-4.91	23
	38	-6	2	-4.88	13
	12	-52	28	-4.81	23
	62	-22	22	-4.78	40
	-44	-10	-2	-4.72	13
	-10	-50	28	-4.70	23
	38	2	16	-4.63	13
	-36	-18	4	-4.27	13
	-18	-32	-14	-4.13	36
	34	18	-28	-4.12	38
	-54	-28	12	-4.11	41
	34	-18	18	-4.03	13
	40	10	-16	-3.98	13
	16	-22	32	-3.66	23
	48	4	-8	-3.55	13
	40	-44	0	-3.47	37
Parietal cortex	-50	-20	20	-3.21	40
	-30	-14	16	-3.19	13
	-52	-76	24	-5.58	39
	4	-38	56	-5.42	5
	28	-36	62	-5.20	1
	-44	-80	34	-4.95	39
	36	-18	46	-4.81	4
	-12	-34	42	-4.76	31
	40	-48	24	-4.03	39
	48	-12	52	-3.99	4
	6	-28	76	-3.98	4
	10	-40	80	-3.96	1
	18	-30	72	-3.96	4
	-36	-22	24	-3.91	1
	40	-30	62	-3.86	1
	-12	-34	56	-3.72	5
	-24	-22	42	-3.69	1
	2	-48	68	-3.68	7
	58	-10	38	-3.50	4
	-68	-20	22	-3.48	1
Occipital cortex	36	-30	42	-3.48	1
	12	-52	62	-3.41	7
	-16	-86	48	-3.15	7
	52	-64	12	-6.04	19
	-14	-48	2	-5.59	18

	12	-86	36	-5.56	19
	-12	-98	22	-5.55	18
	-42	-72	8	-5.48	19
	18	-92	24	-5.16	18
	-20	-68	-2	-5.14	19
	24	-68	0	-5.04	19
	-26	-56	-6	-4.94	19
	30	-50	-4	-4.83	19
	0	-88	26	-4.74	18
	10	-74	2	-4.70	18
	-44	-84	14	-4.61	19
	18	-84	48	-4.32	19
	20	-68	26	-3.58	19
	-54	-78	4	-3.45	19
	-4	-76	26	-3.38	18
Others	22	-16	-18	-7.00	Hippocampus
	-24	-20	-14	-6.39	Hippocampus
	28	8	-20	-4.68	Amygdala
	-30	0	-22	-4.53	Amygdala
	32	-4	-18	-4.43	Hippocampus
	-16	0	-22	-3.46	Amygdala

Supplementary Table 2. Brain regions showing a significant signal increase or decrease in the contrast between incongruent and congruent trials in the Swimmy task. Formats are similar to those in Supplementary Table 1.

Area	x	y	z	z-value	BA
Frontal cortex	-24	-8	50	5.94	6
	-46	6	34	5.49	6
	26	0	54	5.42	6
	-36	-6	66	5.39	6
	-52	8	22	4.64	44
	54	14	36	4.59	44
	42	6	30	4.27	6
	-28	-18	74	3.43	6
	-10	-6	56	3.24	6
	46	-62	-12	7.91	37
Temporal cortex	-46	-64	-6	7.06	37
	-36	-42	42	6.78	40
	48	-38	56	6.12	40
	34	-74	-14	5.78	37
	-42	-50	-14	5.09	37
Parietal cortex	14	-68	58	7.26	7
	-18	-72	56	6.92	7
	28	-58	50	6.81	7
	-24	-72	36	6.57	7
	30	-70	34	6.51	7
	-28	-58	42	6.45	7
	38	-46	54	6.24	7
	-38	-48	54	6.09	7
	-28	-62	60	6.00	7
	-54	-16	52	3.73	1
Occipital cortex	-38	-18	58	3.34	4
	-34	-88	4	7.00	18
	-42	-78	-6	6.90	19
	-32	-86	18	6.66	19
Cerebellum	34	-84	12	6.17	19
	20	-68	-22	6.22	Lobule VI
	16	-56	-44	6.13	Lobule IX
	-30	-58	-24	5.73	Lobule VI
	-18	-68	-24	5.72	Lobule VI
	-42	-58	-26	5.38	Crus I
	6	-78	-28	5.34	Crus II
	2	-66	-18	5.32	Vermis VI
	28	-74	-48	5.14	Crus II
	-32	-40	-34	5.11	Lobule VI
	-6	-78	-26	5.00	Crus I
	-26	-70	-46	4.79	Lobule VIIb
	38	-66	-24	4.78	Crus I
	16	-76	-42	4.76	Crus II
	4	-64	-36	4.75	Vermis VIIa
	34	-48	-26	4.72	Lobule VI
	-16	-42	-44	4.45	Lobule X
	30	-42	-46	4.45	Lobule VIIa
	28	-58	-32	4.43	Lobule VI
	-14	-54	-46	4.17	Lobule IX
	16	-64	-54	4.11	Lobule VIIa

Frontal cortex	-28	-54	-44	4.02	Lobule VIIla
	30	-56	-50	3.87	Lobule VIIla
	-28	-42	-54	3.74	Lobule VIIla
	0	40	-8	-6.45	11
	-28	34	46	-6.26	8
	6	24	-12	-5.93	11
	12	52	14	-5.32	10
	2	52	-8	-5.27	10
	-2	56	28	-5.27	9
	2	10	-14	-5.26	25
	12	38	-8	-5.24	11
	-10	26	-10	-5.22	32
	12	48	26	-5.15	9
	0	-16	44	-5.10	24
	36	4	-18	-4.86	34
	0	56	14	-4.77	10
	-10	28	64	-4.76	6
	28	40	40	-4.74	9
	12	-12	44	-4.69	24
	-14	34	38	-4.66	8
	-16	44	50	-4.66	8
	-36	30	-12	-4.65	47
	50	-6	8	-4.58	6
	6	-14	62	-4.47	6
	0	50	46	-4.38	9
	8	-18	74	-4.35	6
	-4	40	58	-4.18	8
	-22	50	28	-4.13	10
	-10	42	8	-4.10	32
	24	30	60	-4.10	8
	0	32	4	-4.09	24
Temporal cortex	-16	56	12	-3.94	10
	-8	66	18	-3.92	10
	-14	36	20	-3.78	32
	-22	22	-14	-3.60	11
	10	66	6	-3.29	10
	-48	26	-2	-3.25	45
	12	28	50	-3.13	8
	68	-32	14	-6.23	22
	56	-4	-20	-5.87	21
	-8	-48	4	-5.78	30
	60	4	-12	-5.77	38
	-22	-20	-14	-5.69	36
	-40	16	-22	-5.69	38
	10	-54	12	-5.54	23
	-60	-10	-14	-5.32	21
	-58	2	-16	-5.22	38
	36	18	-26	-5.21	38
	46	-16	-4	-5.19	22
	-68	-40	14	-4.99	22
	-12	-30	-6	-4.91	36
	-28	-32	-18	-4.85	37
	-28	10	-20	-4.84	13
	50	22	-18	-4.84	38
	-56	-38	18	-4.76	22
	-42	18	-34	-4.69	38
	-50	14	-14	-4.68	38

	48	-2	-32	-4.56	20
	-42	-22	0	-4.45	41
	-56	4	-4	-4.39	22
	22	-32	-16	-4.26	36
	-68	-32	2	-4.25	21
	38	-26	10	-3.87	41
	12	-50	28	-3.87	23
	-68	-48	2	-3.84	21
	58	-20	-12	-3.79	21
	-24	16	-36	-3.74	38
	-52	-18	-22	-3.70	20
	-40	-4	-14	-3.69	22
	-58	-38	-2	-3.58	21
	-44	-4	-2	-3.58	13
	-44	0	-32	-3.30	38
Parietal cortex	66	-46	14	-5.96	39
	4	-28	60	-5.60	4
	-50	-70	36	-5.36	39
	34	-18	48	-5.30	4
	-2	-32	48	-5.25	31
	0	-44	40	-5.22	31
	38	-22	22	-4.90	1
	-4	-42	56	-4.87	31
	46	-34	22	-4.85	40
	-64	-26	16	-4.75	40
	50	-52	18	-4.69	39
	-6	-54	30	-4.63	31
	-64	-56	16	-4.37	39
	52	-68	42	-4.36	39
	10	-30	74	-4.31	4
	24	-32	64	-4.07	4
	-58	-66	20	-3.98	39
	50	-18	14	-3.97	40
	60	-62	28	-3.97	39
	36	-28	64	-3.96	4
	48	-12	54	-3.85	4
	-36	-20	18	-3.79	1
	64	-52	34	-3.73	39
	-10	-32	76	-3.47	4
	44	-64	34	-3.19	39
Occipital cortex	-8	-94	30	-5.44	18
	14	-46	2	-5.37	18
	16	-92	38	-5.12	19
	6	-86	32	-5.07	19
	-2	-68	22	-4.75	18
	-14	-66	-6	-4.43	19
	-6	-102	18	-4.25	18
	60	-66	8	-4.21	19
	6	-66	2	-4.21	18
	-14	-58	20	-4.15	18
	-14	-42	-8	-3.98	19
	-10	-78	-6	-3.89	18
	22	-56	-4	-3.71	19
	56	-70	20	-3.24	19
	-10	-80	28	-3.19	18
	-32	-52	-4	-3.19	19
	-10	-90	42	-3.03	19

Cerebellum	16	-92	-34	-4.93	Crus II
	-20	-92	-34	-4.26	Crus II
	34	-86	-34	-3.71	Crus II
	-32	-80	-34	-3.48	Crus II
	-20	-78	-34	-3.26	Crus II
	-46	-76	-36	-3.26	Crus I
Others	24	-16	-16	-5.45	Hippocampus
	-22	0	-4	-4.62	Pallidum
	20	4	-18	-4.45	Amygdala
	-32	-38	-6	-4.11	Hippocampus
	-18	0	-16	-4.04	Amygdala
	10	-26	4	-3.72	Thalamus
	20	-6	-6	-3.63	Pallidum

Supplementary Table 3. Brain regions showing a significant interaction effect of response modality (vocal and manual) and congruency (incongruent and congruent) in the Stroop task. Formats are similar to those in Supplementary Table 1.

Area	x	y	z	z-value	BA
Frontal cortex	0	28	64	4.27	6
	18	46	24	4.12	9
	12	60	24	4.11	9
	-58	12	0	3.90	44
	12	24	62	3.74	6
	32	34	24	3.64	9
	46	24	-4	3.63	47
	34	46	20	3.43	10
	0	52	26	3.37	9
	-10	42	34	3.31	9
	-44	20	-6	3.30	47
	-50	-40	18	4.82	22
	64	-28	6	4.59	22
	-60	-20	6	4.16	41
Temporal cortex	58	-10	0	4.01	41
	-62	-8	6	3.69	41
	-64	-40	10	3.67	22
	54	14	-8	3.67	38
	48	-30	2	3.33	22
	68	-12	8	3.20	41
	-64	-42	22	3.16	39
	32	-8	54	-4.11	6
	-10	-2	56	-4.07	6
	-18	-10	70	-3.94	6
	-4	-14	54	-3.55	6
	40	-42	-22	-3.58	37
	-32	-30	52	-4.93	4
	-40	-14	54	-4.68	4
Parietal cortex	-8	-60	58	-4.67	7
	-34	-78	40	-4.27	39
	6	-58	50	-4.16	7
	10	-64	60	-3.07	7
	-34	-72	20	-3.96	19
	-18	-66	26	-3.73	19
	8	-54	-14	-4.53	Lobule V
	40	-42	-34	-3.95	Lobule VI
	24	-42	-20	-3.81	Lobule V
	18	-46	-22	-3.23	Lobule V
Frontal cortex					
Temporal cortex					
Parietal cortex					
Occipital cortex					
Cerebellum					

Supplementary Table 4. Brain regions showing a significant interaction effect of response modality (vocal and manual) and congruency (incongruent and congruent) in the Swimmy task. Formats are similar to those in Supplementary Table 1.

Area	x	y	z	z-value	BA
Frontal cortex	-40	-16	68	-4.83	6
	-4	-12	56	-4.16	6
	-4	-2	48	-4.10	6
	-26	-22	76	-4.08	6
	-14	-16	70	-3.72	6
Temporal cortex	-44	-26	24	-4.30	40
Parietal cortex	-32	-28	62	-5.18	4
	-32	-26	50	-5.15	4
	-46	-22	54	-4.70	1
	-30	-40	64	-4.04	1
Cerebellum	26	-44	-28	-5.25	Lobule VI/V
	18	-52	-18	-3.93	Lobule V

Supplementary Table 5. Brain regions showing differential brain activity in the interference effects (incongruent vs. congruent) between the Stroop and Swimmy tasks. Formats are similar to those in Table 1. *: $P < .05$ corrected across the whole cerebellum.

Area	x	y	z	z-value	BA
Frontal cortex	-38	16	30	4.56	44
	-44	8	52	4.37	6
	-48	14	42	4.18	8
	-40	40	-8	4.04	47
	-2	26	48	3.91	8
	-44	14	12	3.90	44
	-36	30	22	3.57	9
	-42	54	-6	3.55	10
	-2	14	58	3.49	6
	2	32	30	3.34	8
	-50	36	12	3.31	46
	10	24	26	3.31	32
	10	26	64	3.28	6
	-64	-30	0	4.04	21
Temporal cortex	-58	-46	0	3.72	21
	52	-32	-8	3.64	21
	54	-38	8	3.61	22
	72	-34	0	3.56	21
Parietal cortex	-40	-72	50	3.83	39
	-58	-60	36	3.13	39
Cerebellum	34	-74	-42	3.41*	Crus II
	44	-80	-38	3.39*	Crus I
Frontal cortex	22	6	56	-4.33	6
	24	-8	54	-3.53	6
	28	0	68	-3.24	6
Temporal cortex	54	-64	-2	-5.40	37
Parietal cortex	32	-82	34	-5.31	39
	28	-70	44	-4.96	7
	10	-62	64	-4.47	7
	44	-26	36	-4.24	1
	56	-22	46	-3.94	1
	30	-42	48	-3.91	7
	46	-34	62	-3.87	1
	60	-12	38	-3.83	4
	32	-46	68	-3.73	1
	24	-58	46	-3.71	7
	-16	-76	56	-3.51	7
	-24	-82	44	-3.23	7
	46	-76	18	-5.78	19
	-40	-86	14	-5.38	19
Occipital cortex	-52	-74	-2	-4.42	19
	-44	-70	8	-4.32	19
	-26	-70	-12	-4.03	19
	-26	-58	-8	-3.80	19
	-22	-80	18	-3.22	19