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Research report

An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks

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Abstract

The Stroop and Simon tasks typify a class of interference effects in which the introduction of task-irrelevant stimulus characteristics robustly slows reaction times. Behavioral studies have not succeeded in determining whether the neural basis for the resolution of these interference effects during successful task performance is similar or different across tasks. Event-related functional magnetic resonance imaging (fMRI) studies were obtained in 10 healthy young adults during performance of the Stroop and Simon tasks. Activation during the Stroop task replicated findings from two earlier fMRI studies. These activations were remarkably similar to those observed during the Simon task, and included anterior cingulate, supplementary motor, visual association, inferior temporal, inferior parietal, inferior frontal, and dorsolateral prefrontal cortices, as well as the caudate nuclei. The time courses of activation were also similar across tasks. Resolution of interference effects in the Simon and Stroop tasks engage similar brain regions, and with a similar time course. Therefore, despite the widely differing stimulus characteristics employed by these tasks, the neural systems that subserve successful task performance are likely to be similar as well.

Considerable interest has attended the discovery of a general class of neuropsychological interference effects in which reaction times are slowed when irrelevant features of a task are inconsistent with task-relevant ones. The best known of these is the Stroop word-color interference effect [40]. Here the naming of colors is slowed by the simultaneous presentation of a written word, the referent of which is a (task-irrelevant) color that differs from the color of the presented (task-relevant) stimulus. A second well known interference effect is observed in the Simon spatial incompatibility task [8,36,38]. Here the reaction time to identify a target stimulus is slowed when the (task-irrelevant) spatial locations of a target and its (task-relevant) response coding do not correspond, compared with reaction times when spatial location and response coding do correspond. For example, identifying a color or the direction of an arrow with a left- or right-sided key press is faster when the stimulus is presented on the same side as the correct key and slower when the stimulus is presented on the opposite side of the correct key.

These phenomena are of interest in part because the interference with reaction times is among the most robust and replicable cognitive effects yet described. The phenomena are also of interest because they afford the opportunity of parametrically manipulating the stimulus and response characteristics of the task, which in turn may help to define better how the brain processes information and resolves competing task demands. Despite the intense effort and the many hundreds of studies that have been devoted to these task manipulations [26], however, behavioral studies alone have not enjoyed much success in determining how the brain resolves these competing task demands.

The superficial similarity of the interference effects observed across tasks such as the Simon and Stroop have suggested to some investigators that the neural bases for the effects are similar [10,22,44]. Some sophisticated

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behavioral and computational modeling studies have provided evidence that largely supports this claim [17,47], while other evidence weighs against it [37]. Determining whether the neural processes subserving the tasks are similar or distinct has important implications for understanding interference effects and their resolution. If these studies were to determine that the underlying neural processes are in fact different and that they are relatively localized to sensory or motor systems, for example, they would help to confirm conventional theories in which interference arises as a conflict between various portions of the hypothesized serial information processing chains that lead from stimulus to response. Alternatively, determining that the underlying neural processes are similar and that they engage multiple distributed sensory and motor systems would suggest that interference and its resolution might instead arise from supraordinate organizational features of the brain, such as those observed in multiple, parallel distributed processing systems [4].

A number of functional imaging and neurophysiological studies have attempted to define the bases for the interference effects in Simon- and Stroop-like tasks. Functional imaging modalities suggest that multiple, broadly distributed brain regions subserve Stroop performance, including anterior cingulate, inferior parietal, frontotemporal, sensorimotor, and premotor cortices, as well as the basal ganglia [1,3,14,23,24,30,33,42]. In contrast, only one laboratory to our knowledge has yet reported functional imaging findings in a Simon-like task. In an $H_2^{15}O$ PET study of response to laterally presented visual or auditory stimuli using the ipsilateral or contralateral hand, these investigators found large, confluent activations of premotor and dorsal parietal cortices in the contralateral conditions that were largely identical between stimulus modalities (auditory or visual) [19,20]. A role for premotor cortex in helping to resolve the competing demands of this task was supported by a study showing that disruption of premotor cortical function with repetitive transcranial magnetic stimulation produced increased interference effects [34]. In addition, event-related potential studies have suggested that the difference in reaction times for the congruent and incongruent stimuli of the Simon task may be caused in part by the early lateralized readiness potentials over the contralateral premotor region during the lateralized presentation of a (task-irrelevant) target stimulus [45,46]. The existing imaging and neurophysiological studies therefore suggest that the Stroop and Simon tasks engage vastly different neural systems.

Brain activity until now, however, has not been directly compared across the Simon and Stroop tasks in the same imaging study. This comparison would help to determine whether the neural bases for their effects are in fact the same or different. We report an event-related functional magnetic resonance imaging (fMRI) study of the Simon and Stroop tasks. We predicted that we would see brain activation in the Stroop task that was similar to the activation reported in previous Stroop imaging studies and that, furthermore, activation in the Simon task would be similar to that in the Stroop. The Stroop imaging results observed here were nearly identical to those reported in previous fMRI studies [24,33]. The location and time courses of the fMRI activations, and thus of the differential neural activity that the activations are presumed to reflect, were similar across the Stroop and Simon tasks, suggesting that the neural processes that subserve these tasks were also similar.

1. Methods

1.1. Subjects

Five men (26.1±2.9 years old) and five women (26.8±3.1 years old) were recruited from the local community to participate in both fMRI studies. Seven were Caucasian and three (two women) were Asian Americans, and all were native English speakers. All subjects were right-handed and free of previous neurological problems, psychiatric disorders, or head injury. All provided informed written consent and were paid for their participation.

1.2. Stimuli

1.2.1. Stroop task

The stimulus presentation and scanning procedures for the Stroop are presented in greater detail elsewhere [24]. Briefly, a series of colored words was displayed in which a majority of the words were written in the same color as the color denoted by the word (e.g., the word *red* was displayed in red color). These were ‘congruent’ stimuli. A much smaller number of words were written in colors other than that denoted by the word (e.g., the word *green* written in blue color). These were ‘incongruent’ stimuli. Subjects named the color in which the words were presented, irrespective of the meaning of the word that the stimulus denoted. Congruent and incongruent stimuli were presented randomly throughout each scanning session, with the constraint that no word or color of an incongruent stimulus was the same as the preceding word or color. Four colored words (red, green, yellow, or blue) were presented for 1300 ms each, with an interstimulus duration of 350 ms.

Each experiment was composed of 10 runs. Each run was in turn composed of 102 stimuli, with seven of these incongruent and the rest congruent stimuli. Each experiment therefore comprised 68 incongruent events. These were presented pseudorandomly every 13–16 congruent stimuli (i.e., 21.45–26.4 s apart). Each run was 2 min 48 s in duration.

Prior to the scanning session, subjects practiced aloud with one or two runs to ensure a proper understanding of

the task. The interference effect was measured after the scanning session by recording five runs of verbal responses from each subject during presentation of the same stimuli used in the scanner, and with the same stimulus parameters. During the scanning session, subjects were asked to report the number of errors they made after each run.

1.2.2. Simon task

A series of white arrows pointing either left or right was displayed against a black background either to the left or right of a white gaze fixation cross-hair positioned at midline. The majority of stimuli were arrows pointing in the same direction as their position on the screen (e.g., a rightward-pointing arrow presented to the right of midline). These were 'congruent' stimuli. A smaller number of stimuli pointed in a direction opposite their position on the screen (e.g., a left-pointing arrow presented to the right of midline). These were 'incongruent' stimuli. Stimulus presentation was strictly analogous to the presentation of stimuli in the Stroop task. Stimulus duration was 1300 ms and interstimulus interval was 350 ms. Each run was 102 stimuli (2 min 48 s) long, with seven incongruent stimuli presented pseudorandomly every 13–16 congruent stimuli (i.e., 21.46–26.4 s apart). In each run, 51 arrows were left-pointing and 51 were right-pointing, and 51 appeared to the left of midline and 51 appeared to the right. Half of the incongruent stimuli required the same response as the preceding congruent stimulus and half required the opposite response. Each experiment contained 10 runs and 68 incongruent stimuli.

1.2.3. Stimulus presentation

Stimuli were presented against a black background and back-projected onto a screen positioned in front of the subject at the opening of the magnet's bore. Subjects viewed the display through a two-sided mirror mounted above their eyes in the head coil. Subjects who were nearsighted were fitted with corrective lenses so that they could view the screen clearly. All stimuli were presented with PSYSCOPE software [5] running on a Macintosh Power PC (Apple Computer, Cupertino, CA). A digital interface enabled the Macintosh to record the time of acquisition of each image, enabling the synchronization of stimulus presentation with image acquisition (within 20 ms).

In the Stroop task, stimuli were presented directly (0.53°) above the gaze-fixation cross-hair. They subtended 1° vertical and 3.92° horizontal of the visual field. The instructions given to each subject were to silently name as rapidly as possible the color in which the word was written and to avoid making mistakes. Silent naming with minimal or no vocalization was requested to minimize motion and susceptibility artifacts. Naming was used rather than a manual button press because interference effects are reliably greater with verbal than with nonverbal responses [26] and because a button press would have added an additional component to the task (the mapping of color identities to the correct button) that may have complicated interpretation of the source of interference [33].

In the Simon task, arrows were presented to the left or right of the gaze-fixation cross-hair positioned in the center of the subject's visual field. The arrow stimuli subtended 1° vertical and 3.92° horizontal of the visual field. The incongruent stimuli were presented at precisely the same times in each run as were the incongruent Stroop stimuli. Subjects were instructed to respond as quickly as possible to the direction of the arrow by pressing a button on a response box. Subjects pressed a button with their index finger of their right hand, palm down, for a left-pointing arrow and with their middle finger of that hand for a right-pointing arrow. The distance between the left and right response keys equaled that of two adjacent keys on a standard QWERTY keyboard. The button press recorded subject response and reaction time for each trial.

1.3. MRI scanning

Subjects were scanned twice, on 1 day for the Stroop and another for the Simon tasks. The order of scanning was counterbalanced across subjects. Imaging was performed on a GE 1.5 T Signa LX scanner (Milwaukee, WI). Head positioning in the magnet was standardized using the canthomeatal line. A T_1-weighted sagittal localizing scan was used to position the axial images. In all subjects 10 axial T_1-weighted slices were acquired to correspond with 10 axial sections of the Talairach coordinate system [41] oriented parallel to the anterior commissure–posterior commissure (AC–PC) line. The slices were positioned with two slices below, seven slices above, and one slice containing the AC–PC line. Slice thickness was a constant 7 mm, while the skip between slices varied between 0.5 and 2 mm to maintain a strict correspondence with the Talairach coordinate system. Functional images were acquired using a gradient-recalled single shot echo planar pulse sequence, at the same locations as the 10 axial T_1-weighted slices, in runs of 1020 images, or 102 per slice. Repetition time (T_R)=1650 ms, echo time (T_E)=60 ms, flip angle=60°, acquisition matrix 128×64, field of view (FOV)=40×20 cm, slice thickness=7 mm, and in-plane resolution was 3.12×3.12 mm.

1.4. Image analysis

1.4.1. Preprocessing

Studies were visually inspected for artifacts such as ghosting. Images were then motion corrected using SPM 99 software with realignment to the middle image of the middle run. Images were discarded if the peak motion estimates from SPM 99 exceeded 1 mm displacement or 2° rotation [13]. Drift of baseline image intensity was removed using an eighth-order high-pass Butterworth filter with a frequency cutoff equal to 3/4 of the task frequency.

The time series were filtered once forward and once backward to ensure no change in phase of the signal in relation to the phase of the task. Low intensity pixels outside of the brain were removed, and the images were spatially smoothed using a Gaussian filter with a full width at half maximum of 6.3 mm.

1.4.2. Pixel-wise analysis of mean fMRI signal changes

The T_1-weighted axial anatomical images and corresponding echoplanar functional images for each subject were transformed into a common stereotactic space using a piece-wise linear warping to a common bounding box [41]. The pixel-wise average change in fMRI signal associated with the presentation of incongruent stimuli was then calculated for each subject. This was accomplished by first discarding the first two images (representing 3.3 s) following the presentation of each incongruent stimulus in each subject's echoplanar time series to account for the hemodynamic time lag. The average signal of the six images preceding presentation of the incongruent stimuli was subtracted from the average of the next three images following the incongruent stimuli at each pixel. A *t*-statistic was calculated comparing this average signal change across subjects with a value of zero. To account for multiple comparisons, *t*-statistics corresponding with a *P* value <0.005 at nine contiguous pixels [12] were considered significantly activated during presentation of the incongruent relative to the congruent stimuli.

For both the Simon and the Stroop tasks, the comparison of fMRI signals associated with the incongruent and congruent stimulus presentations was fully controlled for the physical features of the stimuli, as well as for orthographic, lexical, and semantic content. The only difference between conditions was therefore the congruence or incongruence of the task-relevant and -irrelevant features of the task. The change in fMRI signal associated with the contrast of the incongruent and congruent stimuli therefore indexed the neural components that were responsible for responding appropriately in each condition and that therefore resolved the interference that the presence of the task-irrelevant features produced. Only trials for which correct responses were recorded during the scanning session were entered into the analyses for the Simon task.

1.4.3. Average signal differences in regions of interest

A priori regions of interest (ROIs) were defined using standard stereotactic coordinates [41], with the exception of one ROI for the thalamus and three for the basal ganglia (caudate, putamen, and globus pallidus), which were hand circumscribed on the T_1-weighted axial anatomical images. Signal changes were then averaged across all pixels within each stereotactically defined ROI. The mean center of mass of activation in each ROI was then reported in Talairach coordinates for each task. This average across pixels served as a measure of the differential regional signal change associated with the behavioral tasks.

1.4.4. Concordance assessment of simon and stroop activations

The similarity of activations across the Simon and Stroop tasks was assessed with a standard statistical test of concordance applied to the set of pixels comprising the entire imaging volume in all subjects. Each pixel in each group activation map was assigned a value of -1, 0, or $+1$ based on its average being a deactivation, non-activation, or activation, respectively, in the group maps at the above-specified thresholds for percent signal change and clustering. Weighted κ coefficients and their 95% confidence intervals were then calculated to assess the concordance of the activation profiles across the two task [11]. κ values can range from -1 to $+1$, with zero indicating a chance level of concordance.

1.4.5. Activation time course

The time course of signal change at each pixel was calculated in relation to presentation of the incongruent stimuli. The time course of each voxel was first smoothed with a Gaussian filter having a full-width at half maximum of 1.98 s. Interpolated adjustments were made in the time course data for the variations in the time of acquisition of each slice during each TR. The average of the six images (representing 13.2 s) preceding each incongruent stimulus was then subtracted from each of the eight images following those stimuli. The time course was plotted for select ROI's that had the largest and most significant activations in each task.

1.4.6. Simon learning effects

In a secondary analysis, we examined the change in signal during each run of the Simon task as a function of change in behavioral interference effects. This should indicate which regions of the brain are involved in learning (and here learning is taken simply to mean improved performance, or progressively reduced interference effects) during successive presentations of the incongruent stimuli. For each run in each subject, the mean difference in reaction time between the incongruent and congruent stimuli was calculated. Also for each run in each subject, fMRI maps of mean signal change for images acquired during the incongruent stimulus presentations were calculated relative to baseline (congruent) stimulus presentations, as described above. This produced 10 maps of signal change and 10 reaction time difference scores for each subject, one for each run. We then constructed for each subject an fMRI map that correlated signal change with reaction time differences across runs at each pixel. The resulting correlation coefficient for each subject was then compared with a value of zero at each pixel using an unpaired *t*-statistic. These *t*-maps were thresholded at a *P* value <0.01 and a cluster filter of nine adjacent pixels. Although these thresholds and cluster filters were not sufficiently stringent to correct fully for multiple statistical

comparisons, they permitted an exploratory assessment of learning effects in the Simon task.

1.4.7. Trial-wise correlations of reaction times with neural activity

In addition to trying to understand how brain activity changes with improving reaction times across runs, we conducted analyses intended to identify the fMRI signal changes that were associated with better performance (i.e., which help to 'resolve interference') during incongruent stimulus trials and that were relatively independent of learning (or practice) effects across runs. We first calculated mean signal change for each correct response to each incongruent stimulus presentation. Then within each run, we correlated this mean signal change with the corresponding reaction time, producing 10 correlation coefficients for each subject (one per run). For each subject, we calculated the average of these 10 correlation coefficients to yield a single average correlation coefficient across runs for that subject to yield a single average for each of the 10 subjects. Finally, we compared the 10 mean correlations (one mean for each of the 10 subjects) with a value of zero to yield at each pixel a *t*-statistic that was thresholded at $P<0.005$ and a cluster filter of nine pixels. This map identified which brain regions had activity that correlated consistently with differential task performance across subjects, and this presumably reflected the resolution of cognitive interference. These analyses were performed only for the Simon study, as on-line measures of task performance during the scan were not available for the Stroop task.

1.4.8. Laterality of stimulus presentation

We assessed whether reaction time in the Simon task differed according to the side on which the stimuli were presented and whether the direction in which the arrow pointed varied according to the side of stimulus presentation. We also examined brain activity during the Simon task as a function of the side on which the stimulus was presented. We first divided the incongruent stimuli into those presented to the left or to the right of midline. Then we compared at each pixel the maps of mean signal change (relative to preceding congruent trials) for stimuli presented on the left with maps of signal change for stimuli presented on the right using a paired *t*-statistic, a pixel-wise activation threshold of $P<0.005$, and a cluster filter of nine pixels.

2. Results

2.1. Behavioral measures

Both tasks demonstrated significant behavioral interference effects. For measures of Stroop interference obtained after the scan, reaction times for incongruent stimuli (848.0±49.5 ms) were significantly longer than for congruent stimuli (549.97±53.6 ms) (paired $t=10.8$, df=9, $P<5\times10^{-6}$). For the Simon task during the scan, reaction times for incongruent stimuli (657.34±79.2 ms) were significantly longer than for congruent stimuli (424.21±39.9 ms) (paired $t=11.87$, df=9, $P<10^{-5}$). Mean reaction times for the subconditions within each of the 10 runs of the scan are shown in Fig. 1a. Subjects made few or no errors during the scanning sessions. The primary behavioral analyses included the following variables: run (1–10), stimulus location (left versus right) and stimulus response (left key versus right key). Reaction times were first analyzed in three-way repeated measures analyses of variance with run (1–10), stimulus location (left or right side), and response (left or right key) as within-subjects factors. This analysis yielded a significant main effect of Run ($F(1,9)=5.90$, $P<0.001$) and the expected Simon effect (i.e., a significant interaction between Location and Response, $F(1,8)=123.27$, $P<0.001$) (Fig. 1b). This analysis also showed no effect of location ($F(1,8)=0.79$, ns) and no effect of response ($F(1,8)=0.06$, ns) on task performance, indicating no asymmetry in performance of the task. A significant interaction between Run, Location, and Response ($F(9,72)=2.81$, $P=0.007$) was observed, indicating that the Simon effect varied

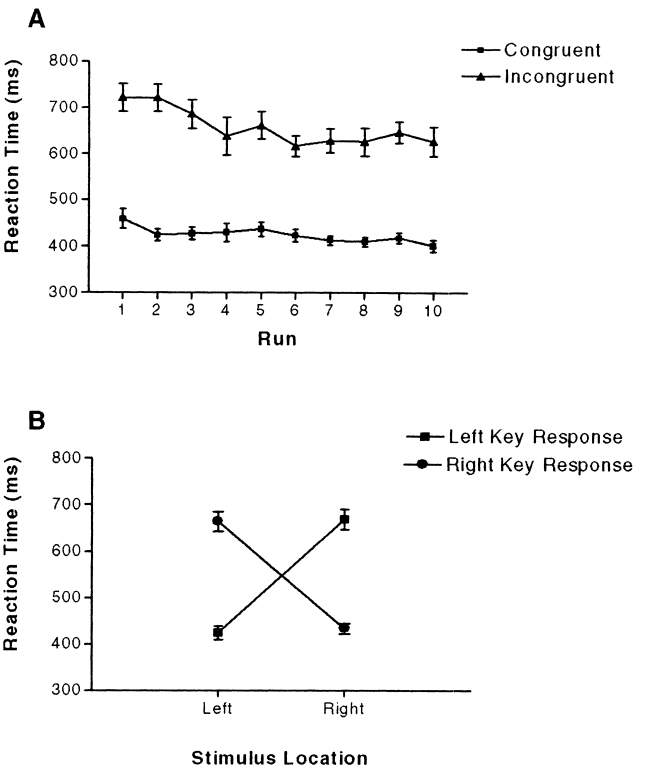

Fig. 1. Reaction times for the Simon effect. In the top figure, mean reaction times are shown for each of the congruent and incongruent stimuli during individual runs of the MRI scan. In the lower figure, mean reaction times are shown for each stimulus location and each response key, demonstrating the expected interaction between stimulus and response for reaction time.

across runs. Including sex or age in the model did not produce significant main effects of sex or age, or significant interaction effects of sex or age with other variables.

2.2. Group average brain activation

The group average activation maps are presented in Fig. 2. The Simon and Stroop tasks produced similar activations. Those regions with the largest activations in common across tasks were tabulated (Table 1), and include supplementary motor (BA 6), visual association (BA 19), anterior cingulate (BA 24), inferior temporal (BA 37), inferior parietal (BA 40), inferior frontal (BA 44), and dorsal prefrontal (BA 46) cortices. A direct, pixel-wise comparison of the Simon and Stroop tasks, also presented in Fig. 2, confirms the similarity in overall pattern of activation across the two tasks, with the Simon tending to activate the superior and inferior parietal regions more strongly than did the Stroop, and the Stroop tending to activate the left dorsoprefrontal and visual cortex more strongly than did the Simon.

2.3. Concordance of activations across tasks

The weighted κ for the concordance of the Simon and Stroop group activation maps was 0.44 (CI 0.38–0.46), indicating moderate concordance for the two maps. Concordance was compromised primarily by the greater activation throughout the parietal lobe in the Simon task.

2.4. Time course analyses

The activation time courses are presented in Fig. 3a,b. The similarity of time courses across tasks is readily apparent. Activation maps of the first 1.65 s following the incongruent event suggested earlier or stronger activation in the Stroop task in the inferior visual association areas (BAs 19 and 37), precuneate (BA 31), and inferior prefrontal regions (BA 44). In contrast, in the 1.65–8.25 s following the incongruent event, stronger activation was observed in the Simon task in the supplementary motor (BA 6), superior parietal (BA 19), and middle temporal regions (BA 21).

2.4. Learning effects

The group average maps for learning effects in the Simon task are presented in Fig. 4. Positive correlations, indicating that signal change lessened as subjects learned (i.e., as interference effects lessened) across runs, were detected in premotor and inferior parietal cortices (BAs 6 and 19) and in the right hippocampus. Negative correlations, indicating that signal changes increased as subjects learned the task, were observed in anterior cingulate, dorsal visual association, and superior parietal cortices (BAs 24, 19, 40), and in the left sensorimotor region.

2.5. Trial-wise correlations of reaction times with neural activity

Negative correlations of reaction time with signal change, indicating greater signal increases during trials with better performance (i.e., associated with faster reaction times and less interference) were seen in the right sensorimotor strip (BA 4) (Fig. 5). Positive correlations of reaction time with signal change, indicating greater signal increases during trials with poorer performance (longer reaction times and more interference) were seen in the left insula, left thalamus, right prefrontal cortices (BAs 10 and 46), right superior temporal region (BA 22), and in the right hippocampus, lingual gyrus, and cuneus (BA 31).

2.6. Laterality of stimulus presentation

Relatively greater activation was seen in the left temporoparietal region (inferior BA 40) and right midbrain during left-sided compared with right-sided presentations of incongruent stimuli (Fig. 6).

3. Discussion

The Simon and Stroop tasks activated the same general brain regions (Fig. 1). These included anterior cingulate (BAs 24 and 32), supplementary motor (BA 6), visual association (BA 19), inferior temporal (BA 37), inferior parietal (BA 40), inferior frontal (BA 44), and dorsolateral prefrontal (BA 46) cortices, and the caudate nuclei. The

Fig. 2. Group average brain activations. Shown here are the group composite *t*-maps for fMRI signal change associated with incongruent compared with congruent stimuli for the Simon and Stroop tasks and for the between-task comparison of signal change. On the left side of the figure are the composites for these maps where at least nine contiguous pixels had P values <0.005. On the right side are the same maps thresholded at $P<0.05$ to emphasize further the similarity of the maps. The more stringent threshold on the left presents the 'tip of the iceberg' of regional activations, which may be somewhat more variable than the subthreshold signal changes. The seemingly greater magnitude and extent of activation during the Simon task than the Stroop (seen in the 'Contrast' columns) could have been caused by a number of factors, including nonphysiological ones such as a more accurate anatomical registration of slices across subjects. Better registration would improve the group average signal-to-noise ratio at each pixel. Some variability in registration across tasks was inevitable due to the need to scan subjects in two separate imaging sessions, each 1.5 h in duration. The Talairach-defined ROIs are represented on each slice with green lines. Brodmann's areas are shown in white numerals on the left-most images. Each transaxial slice is labeled with the Talairach *Z*-coordinate at the far left. Increases in signal during the incongruent relative to congruent events are coded in red or yellow, and decreases are coded in purple or blue. R, right; L, left; cer, cerebellum; ling, lingual gyrus; caud, caudate.

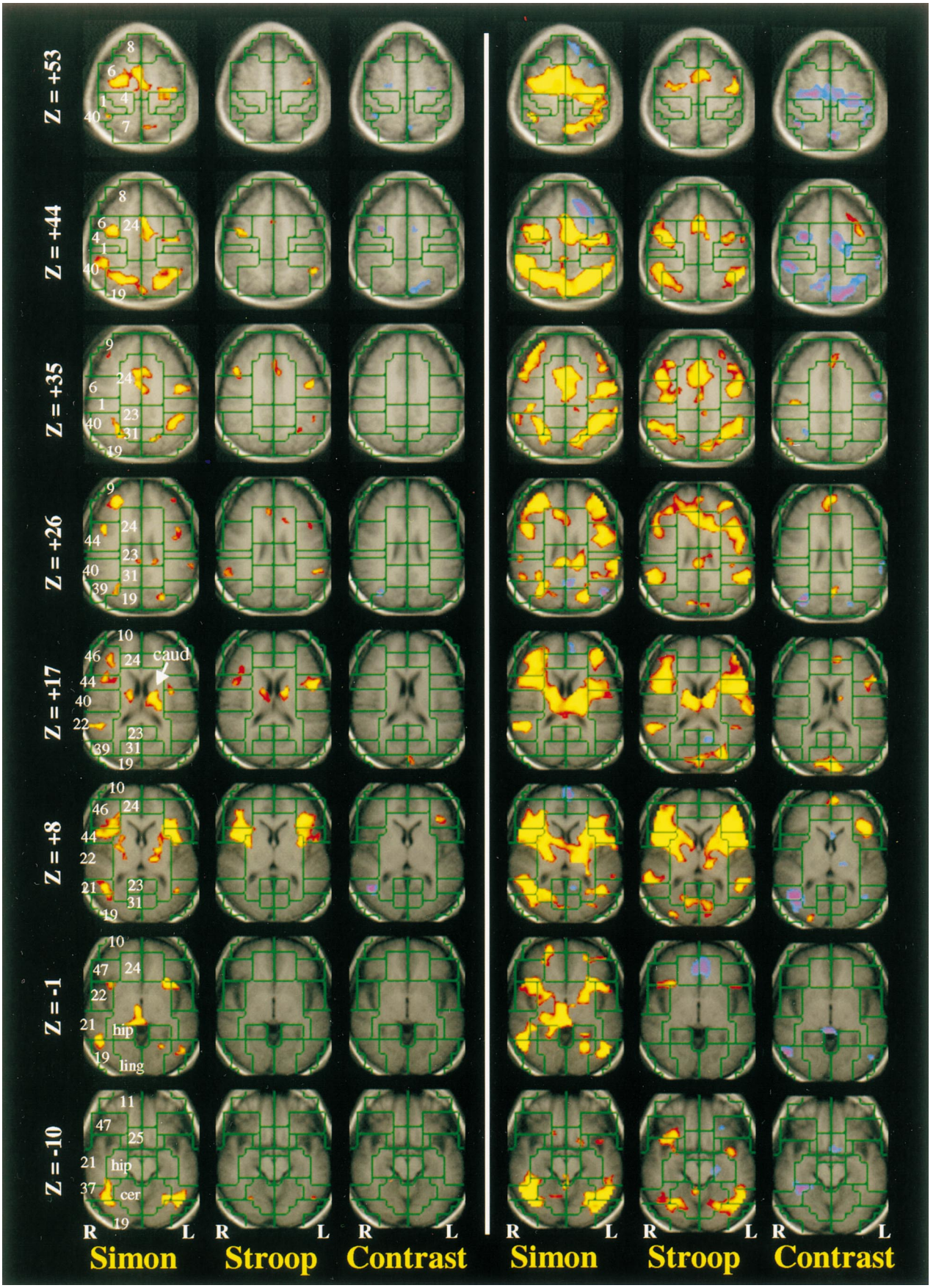
Z = +53
Z = +44
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Table 1
Regional comparison of group average signal change in Simon and Stroop tasks signal change is measured in percent and is averaged across all pixels in a given region

ROI	BA	Side	Simon					Stroop				
			% Signal Δ	S.D.	*x*	*y*	*z*	% Signal Δ	S.D.	*x*	*y*	*z*
Suppl Motor	6	R	0.094	0.32	31.2	0.4	44.6	0.055	0.22	32.3	0.3	42.8
		L	0.063	0.26	−32.2	−3.3	43.2	0.052	0.21	−34.5	−0.4	42.5
Mid Occip Gyr	19	R	0.038	0.32	28.7	−74.5	9.9	0.034	0.19	23.1	−79.3	10.2
		L	0.050	0.30	−28.4	−76.6	8.7	0.049	0.19	−25.7	−78.2	8.0
ACG	24	R	0.037	0.15	11.2	17.2	20.5	0.027	0.16	11.2	17.2	22.0
		L	0.027	0.19	−10.2	13.3	24.4	0.020	0.13	−10.3	15.4	24.3
Inf Temp	37	R	0.121	0.41	43.3	−49.3	−10	0.056	0.33	44.4	−50.4	−10
		L	0.117	0.46	−45.9	−51.9	−10	0.110	0.46	−45.8	−51.4	−10
Inf Parietal	40	R	0.081	0.32	45.0	−37.6	32.4	0.058	0.19	45.9	−37.2	29.3
		L	0.089	0.30	−45.4	−36.7	31.1	0.060	0.20	−46.1	−35.1	27.9
IFG	44	R	0.124	0.42	43.7	7.6	13.2	0.113	0.41	43.6	8.3	12.8
		L	0.115	0.40	−44.3	5.0	13.9	0.143	0.48	−44.6	7.3	13.6
MFG	46	R	0.138	0.50	39.6	32.2	8.9	0.175	0.59	40.6	31.2	8.3
		L	0.093	0.37	−38.8	33.7	8.7	0.157	0.54	−40.5	30.4	7.8

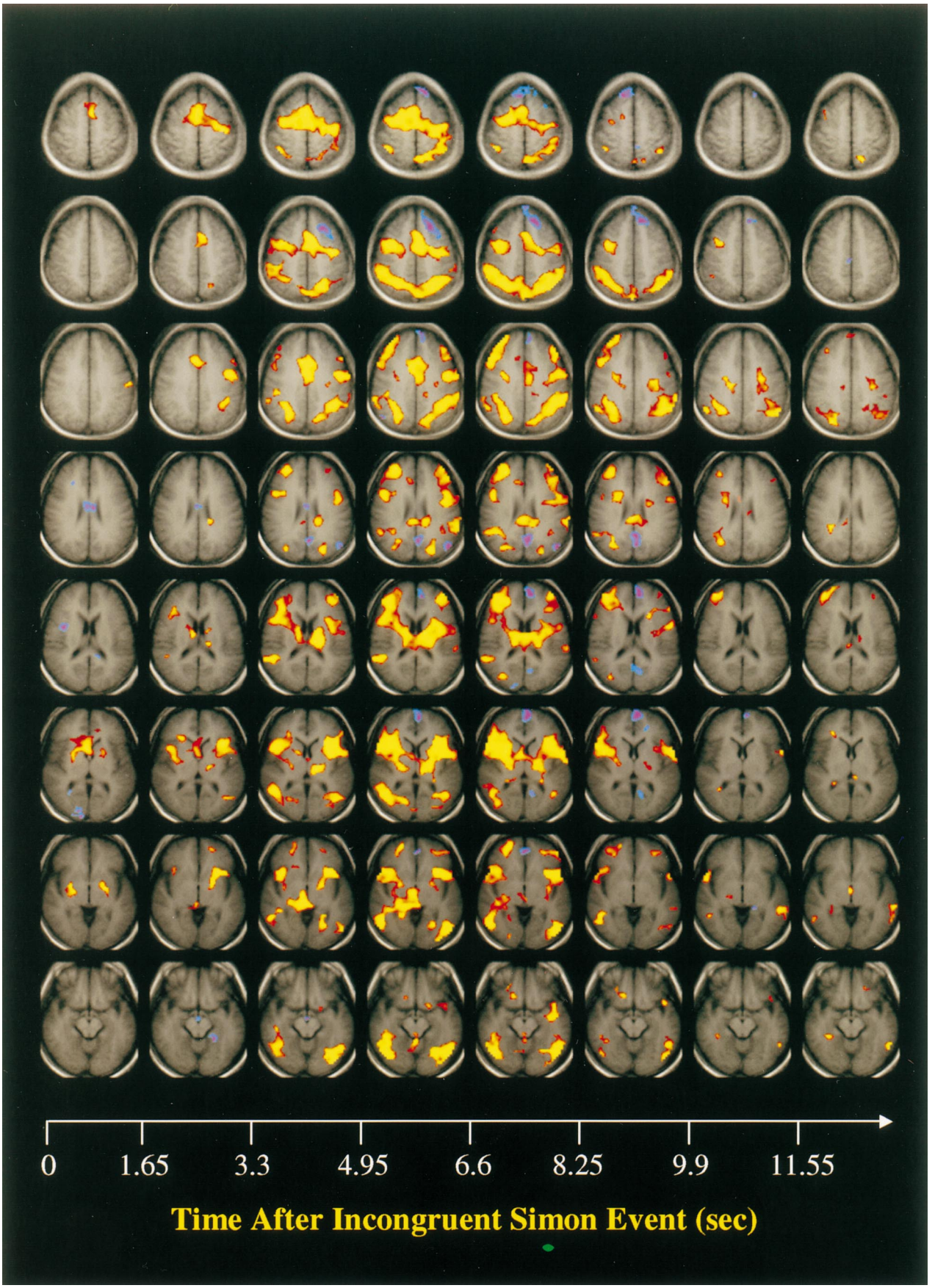
Comparing across regions is difficult because larger ROIs will average signal change across more pixels and will appear artifactually to have smaller average signal change than will some of the smaller ROIs. Comparing mean signal change within a region across tasks or across hemispheres is valid, however, because the size of the region in constant. The *x*, *y*, and *z* columns are Talairach coordinates for the mean center of mass of signal change in each ROI. ROI, region of interest; BA, Brodmann's area; S.D., standard deviation of mean signal change across subjects; Suppl Motor, supplementary motor; Mid Occip Gyr, middle occipital gyrus; ACG, anterior cingulated gyrus; Inf Temp, inferior temporal gyrus; Inf Parietal, inferior parietal region; IFG, inferior frontal gyrus; MFG, middle frontal gyrus.

extent and magnitude of regional activations did vary slightly across tasks, with the Simon task activating supplementary motor (BA 6), superior parietal (BA 19) and superior temporal (BA 21) regions more than did the Stroop, and the Stroop activating dorsolateral prefrontal cortex (BA 46) slightly more than did the Simon. The Stroop activations replicated those reported in two independent samples, one of 34 healthy adults studied in a traditional block design format [33] and another of 10 subjects imaged in an event-related format [24]. Overall, the similarity of the Stroop and Simon maps was striking and suggests that the neural processes that produce appropriate responses to incongruent stimuli relative to congruent stimuli in these tasks are also similar. Quantitative analysis demonstrated that the degree of concordance within subjects and across tasks was far beyond chance.

The similarity of the activation maps of course does not mean that all neural processes that are active during the Stroop and Simon tasks are identical. This is obvious given the differences in stimulus features between the two tasks. Processing of these stimulus features is presumably represented in images acquired during the presentation of the congruent and incongruent stimuli alone, and these features are largely subtracted out when the images acquired during these two conditions are compared with one another. Because the basic stimulus features are well controlled between the congruent and incongruent stimuli in each of the tasks, activation in the fMRI contrast maps represents almost exclusively the neural processes that are required to resolve the interference associated with the incongruent compared with the congruent stimuli. Resolving this interference is, in fact, the defining feature of each of the tasks. A central controversy in work with interference tasks such as these has been whether the neural systems that resolve this interference are the same across tasks. The bulk of the evidence from the group activation maps is that these neural systems are indeed similar. If the systems that resolve the conflict are similar across tasks, then by extension it is likely that the systems giving rise to the interference are also similar across tasks.

The similarity of the time courses of activation for each of these tasks adds to the evidence that the same neural systems resolve their interference effects. Nevertheless, activations were detected somewhat earlier in the Stroop than in the Simon task in the inferior visual association cortices (BAs 19 and 37), precuneate (BA 31), and inferior prefrontal regions (BA 44). This activity was observed within the first 1.65 s after stimulus presentation. Because these regions activated in the Simon task within the next 3 s as well, it is unclear whether these activations in fact activated earlier, or whether they simply activated more robustly in the Stroop and therefore crossed the *t*-threshold

Fig. 3. Time course of activations. Shown here are group composite maps for each repetition time ($T_R = 1.65$ s) of echoplanar image acquisition after presentation of the incongruent stimulus. Minimal activation is seen in the first T_R because of the hemodynamic lag of the blood oxygenation level dependent (BOLD) response. For the Simon task, signal changes associated only with correct responses are shown. The maps depict pixels of nine or more contiguous pixels whose *P* values are <0.05. The *Z*-levels of the transaxial slices are the same as shown in Fig. 1. (a) Simon time course; (b) Stroop time course.


0
1.65
3.3
4.95
6.6
8.25
9.9
11.55
Time After Incongruent Simon Event (sec)

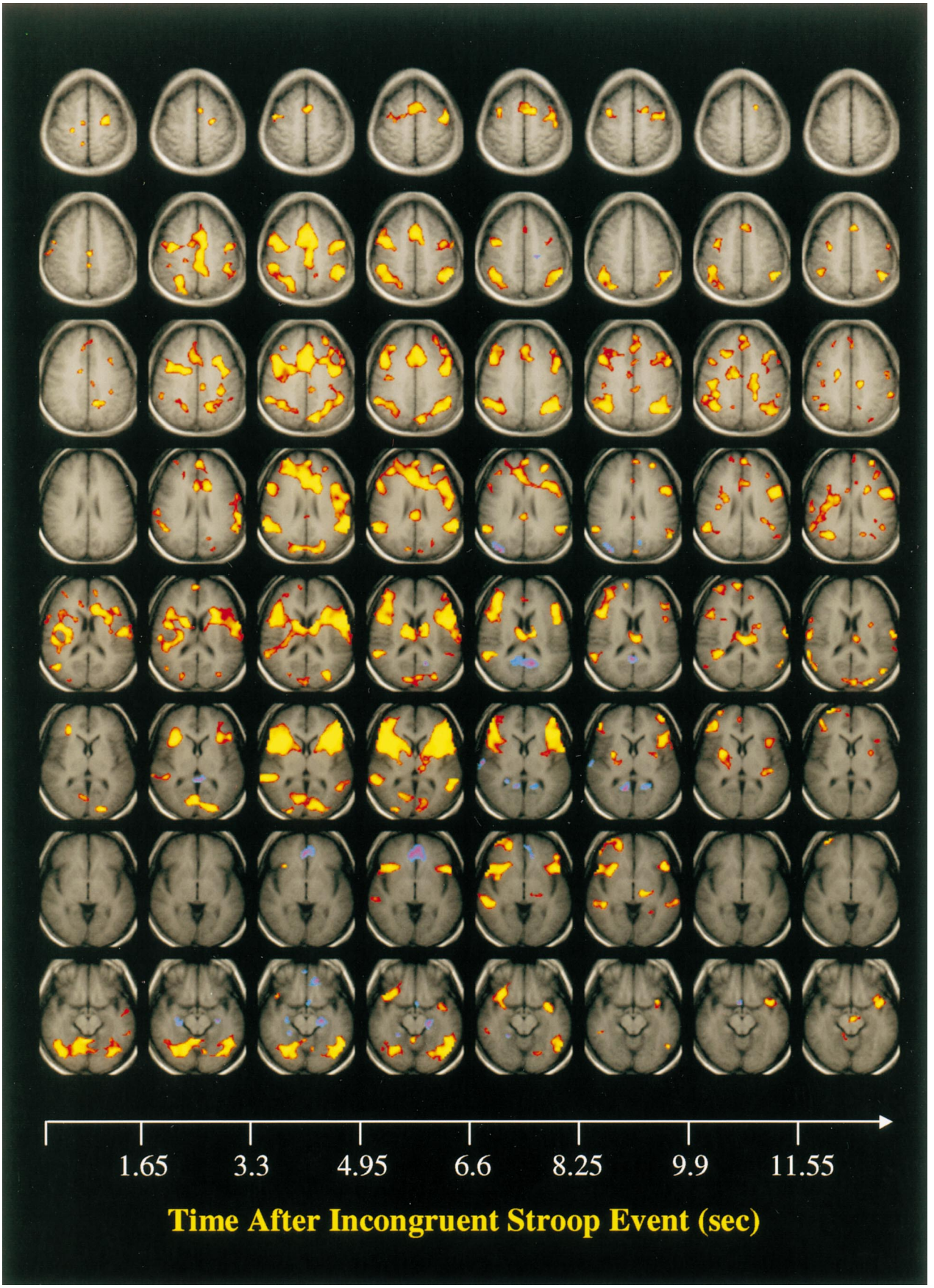


Fig. 3. (*continued*)

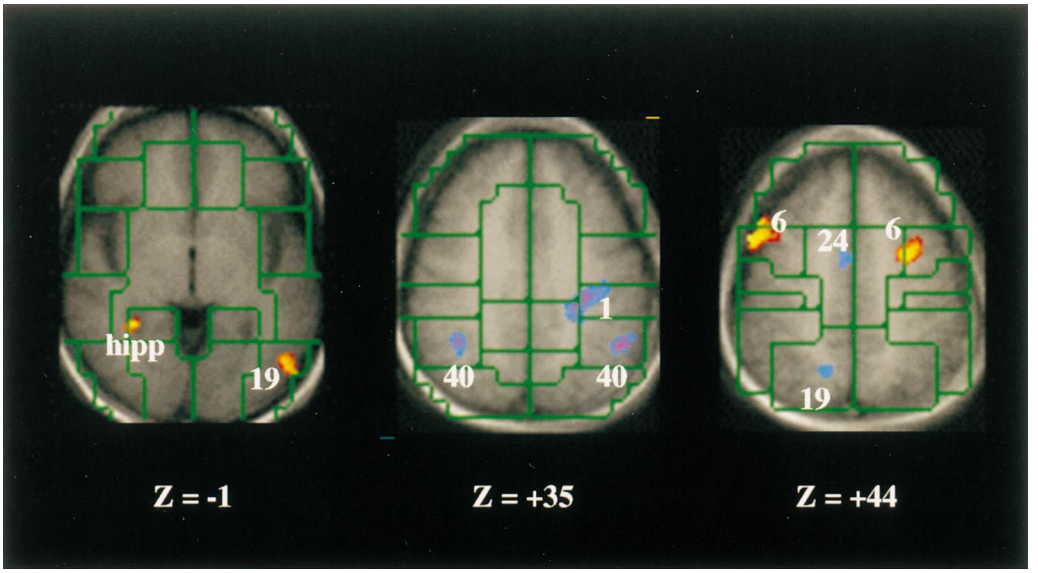


Fig. 4. Learning effects in the Simon task. Pixels at which the mean signal change associated with incongruent stimuli correlated positively with the mean interference effects (the differences in reaction times between incongruent and congruent stimuli) across runs are shown in red or yellow, and pixels at which the correlations were negative are coded in purple or blue. The map is thresholded such that, at nine contiguous pixels, the group average of individual correlation coefficients across runs was different from zero at a P value <0.01. The green lines represent the same Talairach-defined ROIs as in Fig. 1. Brodmann's areas are designated in white numerals.

and cluster filters applied to the activation maps sooner than in the Simon task. Likewise, relatively larger activation in the group average maps for the Simon task was evident in the time course maps in the supplementary motor (BA 6), superior parietal (BA 19), and superior temporal regions (BA 21) 1.65–8.25 s after presentation of the incongruent event (Fig. 2a,b).

We should note that the limited temporal resolution of these activation time courses (1.65 s) is long relative to the time course of neural activity, so that neural events that differ between the Simon and Stroop tasks and that are of shorter duration could be missed with event-related fMRI. Despite the relatively poor temporal resolution of this technology, the time course analyses did demonstrate time-

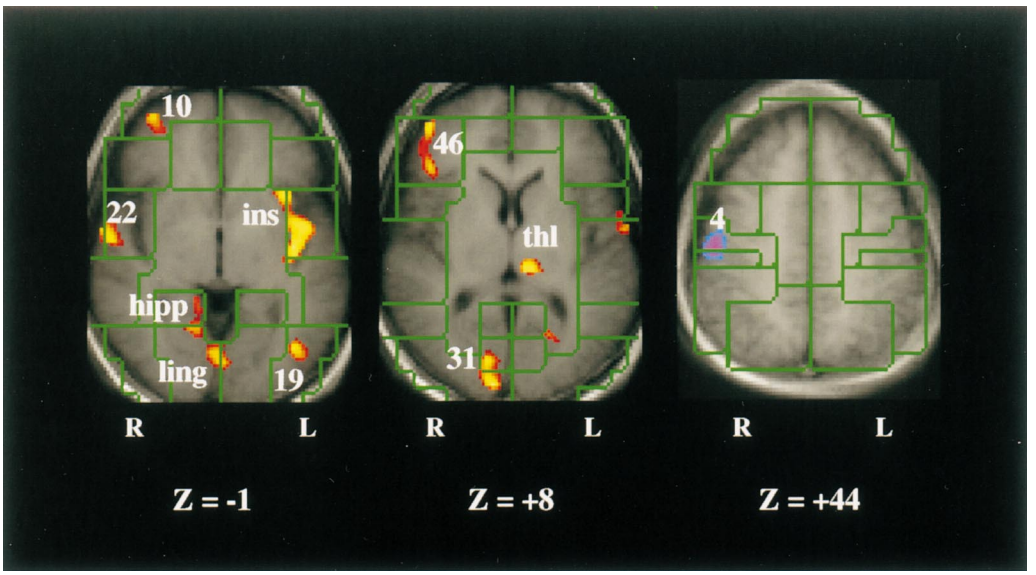


Fig. 5. Trial-wise correlations of reaction times with signal change in the Simon task. Yellow and red represent pixels in which differences in reaction time between individual incongruent trials and the preceding congruent trials correlated positively with signal change at those times. Blue represents pixels in which those correlations were negative. To be displayed, nine contiguous pixels must have reached a statistical threshold of $P<0.005$. Numbers represent Bodmann's areas. ins, insula; thl, thalamus; hipp, hippocampus; ling, lingual gyrus.

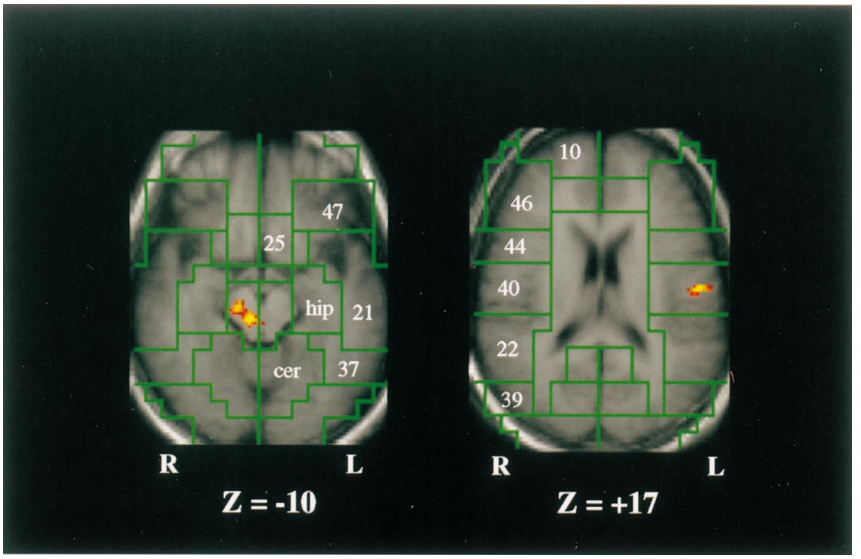


Fig. 6. Laterality of stimulus presentation shown here are the slices on which pixels survived a significance threshold of $P<0.005$ and a cluster filter of nine pixels. Differential signal change was detected in the left temporoparietal region and right midbrain.

varying features in each of the tasks, and these supported the temporal similarity of neural activity in these two tasks at this longer time scale. The question naturally arises as to what these slow changes in neural activity following the incongruent stimuli (i.e., slow changes relative to the speeds of neuronal firing and behavioral response) actually represent. Although data from the present study cannot address this question directly, we suspect that the slow changes in activity represent the automatic alerting, preparedness, and modification of response strategy when the subjects encounter the more difficult and infrequent incongruent stimuli, after responding to relatively long sequences of the easier and more rapidly processed congruent stimulus trials.

We hypothesize that the relatively greater activation in visual association and Broca's regions early in the Stroop time course represents attentional tuning to the naming of the (task-relevant) colors during presentation of the incongruent (task-irrelevant) words of the Stroop stimuli [6,7,9,15,16,18,25,27–29,32,33,35,39]. Similarly, we hypothesize that the more extensive and larger activations in the superior parietal and supplementary motor regions later in the Simon time course likely represent tuning to features, such as spatial location and direction [21], that are unique to the incongruent stimuli of the Simon task and that are known to depend upon these brain regions for perceptual processing. Preliminary findings from the analyses of learning effects in the Simon task are consistent with this hypothesis, in that increasing activity in the anterior cingulate, dorsal visual association, and superior parietal regions in proportion to improved task performance (reduced interference effects) across runs is consistent with the preferential tuning of these spatial processing regions during learning. Once again, however, these same areas were active in both tasks, and their differential activity in the Simon occurred quite early in the activation time course. The regions simply were relatively more active in one task than in the other.

The increasing activation of the anterior cingulate with learning or practice is at variance with some prior studies showing that cingulate activity may decrease with practice [2,31] — although, similar to our findings, cingulate activity has been shown to increase with practice in other studies [43]. These discrepant findings of change in cingulate activity with practice may be accounted for by the fundamental differences in the nature of the tasks employed in these studies and by the varying functional domains of the cingulate that are engaged by those tasks [33]. These varying functional domains within the cingulate may well behave differently during learning or practice. It is also noteworthy that although changes in activity in the cingulate did correlate with mean changes in reaction time across runs of the Simon task, it did not correlate significantly on a trial-by-trial basis with differences in reaction times between congruent and incongruent stimuli within runs. If the latter finding is replicated, it could suggest that the cingulate helps to establish an overall response strategy that improves resolution of cognitive interference and that varies over longer time scales. In contrast, the neural correlates of performance on individual trials in the present study were dominated by increased activity in sensory systems (in visual association areas), affective systems (in the insula), and in attentional or executive systems (in prefrontal regions) when reaction times were prolonged and, by extension, presumably when cognitive interference was experienced as particularly intense.

In conclusion, the similarity of activations and time

courses across the Stroop and Simon tasks suggests that the resolution of cognitive interference that is generated by competing task demands is accomplished by similar, widely distributed functional networks in the brain. The validity of this interpretation is supported by the tight experimental control of stimulus and response properties of the congruent and incongruent trials within each task, which allows us to conclude that the fMRI signal differences across trial types are associated with resolution of the interference from competing task demands, and not with varying stimulus features across the congruent and incongruent stimuli. The similarity of activations and time courses despite the great differences in nature of the stimuli and responses used *across* the two tasks therefore suggests that the activations help to resolve interference, regardless of the specific stimulus and response characteristics *within* each task. Finally, the clear involvement of sensory, motor, and higher executive function areas in resolving these interference effects suggests that serial processing models of the Stroop and Simon effects are likely inadequate to explain fully the neural bases of these phenomena. The resolution of interference in these tasks required neither sensory processing nor response processing regions alone, but rather a broad network of regions across much of the brain. This in turn argues that an alternative information processing model is needed to account for these interference effects and for their resolution.

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