The neural basis of temporal individuation and its capacity limits in the human brain

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The neural basis of temporal individuation and its capacity limits in the human brain. J Neurophysiol 111: 499–512, 2014. First published November 6, 2013; doi:10.1152/jn.00534.2013.—Individuation refers to individuals' use of spatial and temporal properties to register an object as a distinct perceptual event relative to other stimuli. Although behavioral studies have examined both spatial and temporal individuation, neuroimaging investigations of individuation have been restricted to the spatial domain and at relatively late stages of information processing. In this study we used univariate and multivoxel pattern analyses of functional magnetic resonance imaging data to identify brain regions involved in individuating temporally distinct visual items and the neural consequences that arise when this process reaches its capacity limit (repetition blindness, RB). First, we found that regional patterns of blood oxygen level-dependent activity in a large group of brain regions involved in “lower-level” perceptual and “higher-level” attentional/executive processing discriminated between instances where repeated and nonrepeated stimuli were successfully individuated, conditions that placed differential demands on temporal individuation. These results could not be attributed to repetition suppression, stimulus or response factors, task difficulty, regional activation differences, other capacity-limited processes, or artifacts in the data or analyses. Consistent with the global workspace model of consciousness, this finding suggests that temporal individuation is supported by a distributed set of brain regions, rather than a single neural correlate. Second, conditions that reflect the capacity limit of individuation (instances of RB) modulated the amplitude, rather than spatial pattern, of activity in the left hemisphere premotor cortex. This finding could not be attributed to response conflict/ambiguity and likely reflects a candidate brain region underlying the capacity-limited process that gives rise to RB.

individuation; consciousness; repetition blindness; multivoxel pattern analysis; attention

Behavior is shaped by how individuals perceive their external environment. Because our environment provides far too much sensory information for all of it to be processed up to awareness, we rely on selective attention mechanisms to reduce the overwhelming amount of available information to a manageable set of relevant items and/or sources (Pashler 1998). Merely attending to sensory information, however, does not guarantee that it will reach awareness or impact behavior, because such information needs to be encoded in relation to the observer’s preexisting rules, goals, and knowledge (Cohen et al. 2012).

In vision, a key operation implicated in successful object encoding is “individuation,” the process by which observers use spatial and temporal episodic cues to determine where and when an object appeared (e.g., Chun 1997; Kahneman et al. 1992; Mitroff et al. 2007; Pylyshyn 1989, 1994; Xu and Chun 2009). This process is crucial for registering individual items as distinct perceptual events and is thought to underlie observers’ impaired ability to discriminate between separate occurrences of objects with the same identity relative to those with different identities (Kanwisher 1987). Although observers show capacity limits associated with individuating items across both time and space (e.g., Kanwisher 1991; Kanwisher and Potter 1989; Luo and Caramazza 1995, 1996), and previous studies have begun to identify the neural correlates of spatial individuation (e.g., Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007), no study has identified the neural substrates underlying temporal individuation. In the present study we used functional magnetic resonance imaging (fMRI) to investigate the brain regions and mechanisms that are involved in the successful individuation of temporally distinct objects during encoding and how disruptions to this process are represented in the brain.

Initial fMRI investigations into individuation have identified a candidate brain area that might store individuated object representations in visual short-term memory (Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007). Specifically, Xu (2009) found that activity in the inferior intraparietal sulcus (IPS) was sensitive to the number of previously individuated items, regardless of the overall number of perceptual features. This finding suggested that the inferior IPS is involved in storing spatially individuated items and that activity in this region could be dissociated from that in other regions involved in storing object identities. On the basis of their findings, Xu and Chun (2009) proposed the “neural object-file” account, which argues that object individuation is supported by the inferior IPS.

Although Xu and colleagues’ investigations suggest a neural basis for spatial individuation, their work focused on a few posterior brain regions and did not explore the contributions of other “higher-level” brain areas. Since recent models of consciousness propose that awareness involves a distributed set of psychological processes and neural substrates (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004), individuation could be underpinned by a more diffuse group of regions. In addition, the inferior IPS appears to store individuated representations, yet storage reflects the consequences of individuation rather than the generation of such representations. Here, we are interested in the brain regions that are involved in actively individuating an object during encoding. To address this issue, we directly compared 1)
 conditions that place high or low demands on temporal individuation processes during encoding and 2) conditions of successful vs. unsuccessful registration of identical stimuli. To explore the possible role of a more diverse set of regions, our analyses compared changes in blood oxygen level-dependent (BOLD) activity across a wide set of cortical areas.

We employed the repetition blindness (RB) phenomenon to investigate temporal individuation. RB refers to the finding that observers are poorer at reporting two targets embedded in a rapid serial visual presentation (RSVP) if they have the same identity, relative to different identities (Kanwisher 1987; Park and Kanwisher 1994). Kanwisher’s (1987) prominent account of RB argues that token information (spatiotemporal properties of an object) for the second target cannot be bound to its type representation (featural and conceptual properties of an object) when it activates the same type as the first target within a short space of time. RB does not reflect a failure to create a type or token for a repeated item, but rather reflects a limitation associated with binding these two representations for conscious report. This deficit is thought to reflect a capacity limit of individuation, because it is strongest when the two targets appear within close temporal or spatial proximity (e.g., Chun 1997; Kanwisher 1987). Kanwisher’s account views RB as a perceptual phenomenon, yet other models propose that RB has a later locus, reflecting a retrieval bias or failure (Fagot and Pashler 1995; Whittlesea and Masson 2005). However, because RB has been observed in tasks that have very low memory demands or require immediate responses, there appears to be a significant perceptual component to the effect (e.g., Anderson and Neill 2002; Dux and Marois 2007; Johnston et al. 2002).

We therefore used a RB paradigm to vary the trial-level demands of successfully individuating two sequentially presented stimuli as distinct items by manipulating whether the critical items had the same or different identities. This approach allowed us to investigate two novel questions: First, can temporal individuation be localized to a single brain region (see Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007), or does this process arise from widespread encoding throughout the brain, as suggested by recent models of consciousness (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004)? We expected that activity in brain regions involved in temporal individuation would be modulated by the demands placed on this process, whereby it is more demanding to successfully individuate repeated stimuli than nonrepeated stimuli. Second, what neural consequences arise when demands exceed the capacity limit of the individuation process, as reflected by the behavioral RB deficit? We predicted the brain areas that underpin capacity limits that lead to RB would respond differently under conditions where two repeated stimuli were successfully detected compared with when they were not.

MATERIALS AND METHODS

Participants

We recruited 16 volunteers for 2 behavioral experiments (n = 6 and 10, respectively; 2 males in each) and 28 volunteers for an fMRI experiment (12 males). The mean ages for participants in the 3 experiments were 26.0 (SD 5.2), 18.8 (SD 1.0), and 23.8 (SD 3.7) yr, respectively. Participants were compensated for their time with course credit or payment. Data from five participants were excluded from the fMRI experiment due to excessive head motion (motion >4 mm/deg in any translational direction or rotation, respectively; henceforth, n = 23). All participants had normal or corrected-to-normal vision. Four participants from the first behavioral experiment also participated in the fMRI experiment. The University of Queensland Ethics Committee approved the protocol for all the experiments.

Stimuli

The stimulus set used in all the experiments consisted of 56 indoor and 56 outdoor scenes and scrambled versions of each scene (Marois et al. 2004). All stimuli were presented in grayscale and subtended 11.8° × 11.8° of visual angle at the viewing distance of 57 cm outside the scanner (scene stimuli measured 6.5° × 6.5° of visual angle inside the scanner, viewed from a distance of 90 cm). In the fMRI experiment, we also used 18 photographs of faces from the NimStim face database (Tottenham et al. 2009) for the localizer task. Face stimuli were presented in grayscale and subtended 5.2° × 6.5° of visual angle inside the scanner. Experiments were programmed in MATLAB with the Psychophysics Toolbox (Brainard 1997; Pelli 1997).

Behavioral Experiments

Long intertrial interval RB experiment. We first developed an RB paradigm optimized for fMRI (Fig. 1). This paradigm was based on similar studies that have used pictures or novel objects as stimuli (e.g., Coltheart et al. 2005; Harris and Dux 2005a, 2005b). The purpose of the first behavioral experiment was to assess whether our protocol could elicit the standard RB behavioral effect. Each trial began with a fixation cross for 500 ms, followed by an RSVP stream consisting of a forward scrambled scene mask, three sequentially presented intact scenes (first critical scene, C1; distractor scene; second critical scene, C2), and a backward scrambled scene mask (100 ms/item). We manipulated “scene repetition” within participants such that both critical scenes had either the same identity (repeat) or different identities (nonrepeat). Participants were informed that the distractor scene would never be the same as C1 or C2.

At the end of the RSVP stream, a blank response screen was presented for 3 s, followed by an 8-s intertrial interval (ITI; i.e., a slow event-related fMRI protocol). The participants’ task was to report one of three response options during the posttrial 3-s window: They could report that a scene was repeated, no scene was repeated, or only two scenes were presented (catch trial response; see below). Only response accuracy was emphasized. We also ran a behavioral experiment using this RB paradigm without the long ITI (the next trial began immediately after participants made an undimed response), and the pattern of results was comparable to the present experiment (reported below). We chose to use a paradigm in which participants had to detect the presence of a repetition, rather than identify the critical items, because this was more appropriate for studying RB in the scanner with scene stimuli (i.e., responses were forced choice and could be made using a button box). It should be noted that both detection and identification approaches have been used to study RB previously (e.g., Hochhaus and Johnston 1996; Kanwisher et al. 1996; Park and Kanwisher 1994) and are considered to tap the same individuation processes.

As is standard in behavioral investigations of RB, catch trials represented 20% of trials to reduce the likelihood of participants guessing “repeat” on trials where they missed the second repeated scene (Dux and Coltheart 2008; Harris and Dux 2005a, 2005b). These trials only contained two different intact scenes in the RSVP stream. To ensure catch trials lasted for the same duration as repeat and nonrepeat trials (12 s), we included an additional fixation screen for 100 ms between the response window and ITI (see Fig. 1).

Participants were provided with an instruction sheet outlining the task and response keys and completed 20 practice trials before the testing. There were 6 blocks of 25 test trials with an equal number of repeat and nonrepeat trials. The order of the trial types was random.
Behavioral experiments were completed on a 20-inch Dell Trinitron CRT monitor with a refresh rate of 100 Hz using a Macintosh mini computer.

**Lag RB experiment.** We conducted a second behavioral experiment to ensure that our RB paradigm specifically tapped the temporal capacity limits of individuation. The attentional blink (AB) is similar to RB because it too occurs under dual-target RSVP conditions, is characterized by poorer identification of a second target at short intertarget intervals (e.g., 200–500 ms), and is thought to reflect a failure of perceptual awareness (Chun and Potter 1995; Raymond et al. 1992). The AB, however, occurs under conditions where the two targets have different identities. Thus, in contrast to RB, the AB reflects the temporal capacity limits of object identification, rather than individuation (Chun 1997; see also Dux and Marois 2009). In an additional behavioral experiment, we confirmed that the observed differences in detection accuracy on repeat and nonrepeat trials in the long ITI RB experiment reflected the temporal capacity limits of individuation, rather than identification.

This lag RB experiment was similar to the first behavioral experiment, except we also manipulated the temporal “lag” between C1 and C2 (2, 3, 5, or 7 items). Each RSVP stream consisted of 3 intact scenes (C1, distractor, C2) and 12 scrambled scenes. C1 and the distractor scene always appeared at the sixth and seventh serial positions, respectively. C2 would appear immediately following the distractor scene (lag 2) or after one (lag 3), three (lag 5), or five (lag 7) intervening items. The lag 2 condition had the same temporal gap between C1 and C2 that was used in the long ITI RB experiment and reflects the condition in which the RB deficit is most severe (e.g., Kanwisher 1987; Park and Kanwisher 1994). All scrambled scenes were different. Catch trials were identical to repeat and nonrepeat trials, except C2 was replaced with a scrambled scene, meaning that only two intact scenes were presented. Because this version of the RB paradigm was not used with fMRI, we removed the timed response window and long ITI. Participants responded when prompted at the end of the stream. There were 12 practice trials and 6 blocks of 50 test trials.

**fMRI Experiment**

In the fMRI experiment, we used the long ITI RB paradigm to manipulate the conditions under which temporal individuation occurred. BOLD activity in response to this task was measured across the whole brain, with a focus on a set of lower- and higher-level a priori regions of interest (ROIs; see below). This paradigm included 200 trials split over 8 event-related runs, with 80 repeat, 80 nonrepeat, and 40 catch trials. Each run consisted of a 20-s fixation period followed by 25 RB trials and then a 12-s fixation period. Participants responded by pressing one of two buttons on a button box in their right hand for repeat and nonrepeat responses or one button with their left hand for catch responses. The order of trial types was random, and the number of trials for each condition was equal across runs.

**Localizer task.** After the RB runs, participants completed the localizer task. Participants were presented with separate 20-s blocks of fixation, face, and scene stimuli. At the beginning of each stimulus block, a visual cue was presented for 2 s to indicate the block type. Each block included nine trials in which an intact scene or face was presented for 1 s, followed by a 1-s ITI. On half the scene and face blocks, participants were cued to passively view the stimuli (“passive scene” and “passive face”). On the remaining blocks, participants were cued to classify the scenes as indoor or outdoor scenes (“task
There were two localizer runs where each consisted of four blocks of fixation and three blocks of each of the stimulus block types. The order of the stimulus blocks was random without replacement, and a fixation block was presented after every four stimulus blocks. An additional 8-s fixation period was presented at the start and end of each localizer run.

Data acquisition. Images were acquired using a 3T Siemens Trio MRI scanner (Erlangen, Germany). Participants lay supine in the scanner and viewed the visual display via rear projection onto a mirror mounted on a 12-channel head coil. A T1-weighted anatomic image was collected in the middle of the scanning session using an MPRAGE sequence [repetition time (TR) = 1.9 s, echo time (TE) = 2.32 ms, flip angle (FA) = 9°, field of view (FOV) = 192 × 230 × 256, resolution = 1 mm³]. Functional T2*-weighted images were acquired parallel to the anterior commissure-posterior commissure plane using a GRE EPI sequence (TR = 2 s, TE = 25 ms, FA = 90°, FOV = 192 × 192, matrix = 64 × 64, in-plane resolution = 3 × 3 mm). Each volume consisted of 33 slices (thickness = 3 mm, interslice gap = 0.3 mm), providing whole brain coverage. We synchronized the stimulus presentation with the acquisition of functional volumes. There were 166 and 168 volumes (including 4 dummy volumes) acquired for each of the event-related and localizer runs, respectively.

Data analyses. We analyzed our data using Brain Voyager QX software (Brain Innovation, Maastricht, The Netherlands) and custom MATLAB code.

PREPROCESSING. Data preprocessing included three-dimensional (3-D) motion correction (where each functional image was aligned to the first run), slice-scan time correction, and high-pass temporal filtering (3 cycles per run). All functional images were coregistered to the anatomic scan and transformed into standardized space (Talairach and Tourmoux 1988). No spatial smoothing was applied to preserve fine-grained spatial information for the multivoxel pattern analyses (MVPA; see below).

REGIONS OF INTEREST. We first isolated a group of 20 ROIs (Table 1). These regions consisted of perceptual areas involved in processing scenes (parahippocampal place area, PPA; Epstein et al. 2003) and objects (lateral occipital complex, LOC; Kourtzi and Kanwisher 2001), regions previously implicated in object individuation and identification (see Xu 2009), and higher-level attentional/executive areas associated with capacity limits of information processing (Dux et al. 2006, 2009; Heekeren et al. 2004; Jiang and Kanwisher 2003; Marois et al. 2006; Schubert and Szameit 2003; Szameit et al. 2002). Given the extensive overlap between the superior parietal lobule and superior IPS ROIs in the majority of subjects, we collapsed univariate and multivariate results across these two parietal regions (denoted as sIPS/SPL); hence, 18 ROIs were examined.

To localize these ROIs in each participant, we submitted data from the localizer runs to single-participant general linear model voxelwise analyses using a statistical threshold of \( q < 0.05 \) (false discovery rate, FDR). We defined regressors for the fixation, passive face, task face, passive scene and task scene blocks, which were then convolved with a double-gamma hemodynamic response function. To isolate the PPA, we contrasted activity between scene and face stimuli blocks. The scene perception ROIs were localized by contrasting activity between scene and face stimuli blocks. No. of participants data indicates the number of participants for whom an ROI was successfully identified. Talairach coordinates \((x, y, z)\) represent the mean Talairach for each brain region with SD in parentheses. IFJ, inferior frontal junction; ACC, anterior cingulate cortex; SMFC, superior medial frontal cortex; DLPPC, dorsal lateral prefrontal cortex; PMC, premotor cortex; SPL, superior parietal lobule; sIPS, superior intra-parietal sulcus; IPS, inferior intraparietal sulcus; LOC, lateral occipital complex; PPA, parahippocampal place area. L, left; R, right; Bi, bilateral.

For the univariate analysis, an ROI included all voxels above a statistical threshold surrounding the peak voxel up to a maximum of \( 6 \times 6 \times 6 \) mm (8 voxels). For the multivariate analysis, ROIs were defined by a \( 15 \times 15 \times 15 \) mm and \( 21 \times 21 \times 21 \) mm cube (125 and 343 voxels, respectively), centered on each individual participant’s Talairach coordinates of the peak voxel. We used larger ROI sizes to increase variance across voxels and to be consistent with other studies that have employed this analytic technique (e.g., Gallivan et al. 2011; Harrison and Tong 2009; Kamitani and Tong 2005; Oosterhof et al. 2012). We defined ROIs for the multivariate analyses using two different sizes to ensure that decoding results were reliable, regardless of the particular number of voxels included in the analysis (Spiridon and Kanwisher 2002). We only report the MVPA results for ROIs defined by a \( 21 \times 21 \times 21 \) mm cube, but our findings were consistent across both ROI sizes unless otherwise stated.

UNIVARIATE ANALYSIS. We first analyzed data from the RB event-related runs using a standard univariate approach. Time courses for each condition, ROI (with signal averaged across all voxels in the ROI), and participant were extracted. Percent signal change was calculated relative to signal during the volume preceding trial onset. This baseline was chosen to exclude any potential activity associated with the previous trial. Individual participant time courses were averaged across all participants, and we compared differences in peak amplitude between the experimental conditions. Peak amplitude was
defined as the averaged signal across time points 4–8 s post-trial onset. Statistical significance was assessed using repeated-measures t-tests and a statistical threshold of $P < 0.05$ (Bonferroni corrected for the 18 regions tested).

**MULTIVARIATE ANALYSES.** To increase the sensitivity of our analysis, we also analyzed our data using MVPA (Haynes and Rees 2006; Kriegeskorte et al. 2006). This analytic approach is more sensitive than univariate methods because it examines differences in activity across multiple voxels, rather than each voxel individually. Indeed, activity within any single voxel might show weak differences between conditions if only a small proportion of neurons in that voxel code for information associated with the experimental task. MVPA attempts to improve the sensitivity of fMRI analysis by pooling these weak, but reliable, signals across voxels and comparing conditions based on the resulting ensemble patterns of activity. MVPA was implemented using custom MATLAB software and a linear support vector machine binary algorithm (Chang and Lin 2011).

For each voxel in a given ROI, we extracted the average percent signal change corresponding to the peak of the time course for each trial (4–8 s post-trial onset). Before each MVPA, data for each voxel in an ROI were z-transformed and mean-centered by subtracting the condition mean for the entire ROI from the response in each individual voxel to control for overall differences in signal amplitude between conditions (see Esterman et al. 2009; Tamber-Rosenau et al. 2011). We trained a series of binary classifiers to discriminate between patterns of activity associated with the experimental conditions using the leave-one-out cross-validation method. In each fold, one run was used to test the classifier’s generalization performance and the remaining seven runs were used to train the classifier. Decoding accuracy for each ROI was averaged across each cross-validation loop and tested against chance accuracy (50%) using one-sample t-tests and a statistical threshold of $P < 0.05$ (Bonferroni corrected for the 18 regions tested). If there is a functional distinction between pools of neurons within a given ROI that respond to each condition, then the classifier should be better than chance at discriminating between patterns of activity on the test trials (Pereira et al. 2009).

We also performed a searchlight analysis to explore whether other regions outside our ROIs showed a similar pattern of results to the ROIs we tested (Kriegeskorte et al. 2006). A spherical searchlight ROI with a 2-voxel radius (33 voxels) was centered on every voxel of the volume. We used the same cross-validation classification method procedure as the ROI analysis to test for information contained in these local activity patterns. Classification accuracy for each searchlight was assigned to the central voxel and compared against chance performance to test for significance ($q < 0.05$, FDR).

**RESULTS**

All statistical analyses were conducted with a two-tailed alpha level of 0.05, and Bonferroni correction was applied for multiple comparisons unless otherwise stated.

**Behavioral Experiments**

Chance performance in the RB task was 33.3%. To first assess whether our paradigm could elicit the standard RB behavioral effect, we submitted the mean detection accuracy data from the long ITI RB experiment to a repeated-measures t-test. Detection accuracy reflects the percentage of trials in which participants correctly detected the identity of the two critical scenes (e.g., a “repeat” response on repeat trials; “non-repeat” or “2 scene only” responses would be considered incorrect on this trial). Consistent with other RB studies that have used a paradigm similar to ours (e.g., Hochhaus and Johnston 1996; Kanwisher et al. 1996; Park and Kanwisher 1994), participants were significantly less accurate on repeat trials relative to nonrepeat trials: $t(5) = 2.93, P = 0.033$ (see Fig. 2A). In subsequent experiments conducted in our laboratory, we have replicated this RB result using alphanumeric stimuli, suggesting that this behavioral effect is not specific to the type of stimulus used. Performance on catch trials was around chance in this experiment [mean 36.7%, SD 8.2%; $t(5) < 1$], where participants’ erroneous responses were more likely to be a nonrepeat response than a repeat response (69.6 vs. 25.2% of errors, respectively; the remaining 5.2% of errors were absent responses). This proportion and pattern of catch trial errors are consistent with previous RB studies (Dux and Coltheart 2008).

Data from the lag RB experiment were used to test whether our RB paradigm specifically tapped the temporal capacity limits of individuation, rather than identification. If our paradigm elicited identification limitations, we expected participants would be poorer at detecting both repeated and nonrepeated scenes at shorter temporal lags, relative to longer temporal lags. On the other hand, deficits in individuation indicate a specific difficulty in registering two repeated items as separate items. Thus, if our paradigm only tapped the temporal capacity limits of individuation, we predicted detection of repeated scenes alone would be affected by lag.

To assess this, we submitted mean detection accuracy data from the lag RB experiment to a 2 (scene repetition: repeat, nonrepeat) by 4 (lag: 2, 3, 5, 7) repeated-measures ANOVA.
significant main effect was found for both scene repetition \( F(1, 9) = 5.51 \), mean squared error (MSE) = 394, \( P = 0.044 \), \( \eta^2_p = 0.38 \) and lag \( F(3, 27) = 4.44 \), MSE = 75, \( P = 0.012 \), \( \eta^2_p = 0.33 \) (see Fig. 2B). Crucially, a significant interaction between these two factors also emerged \( F(3, 27) = 6.28 \), MSE = 169, \( P = 0.002 \), \( \eta^2_p = 0.41 \). Follow-up t-tests revealed detection accuracy on repeat trials was significantly reduced at shorter lags (lags 2 and 3) relative to longer lags (lags 5 and 7) \( t(9) = 5.55 \), \( P < 0.001 \), but detection accuracy on nonrepeat trials did not vary with lag \( t(9) = 1.31 \), \( P = 0.222 \). Thus our RB paradigm specifically tapped temporal capacity limitations associated with individuation, rather than identification. These findings demonstrate that the present paradigm elicited a pure RB effect that was not confounded by the AB. Similar to the first behavioral experiment, catch trial performance was no greater than chance [mean 24.5%, SD 16.2%; \( t(9) = 1.72 \), \( P = 0.119 \)].

**fMRI Experiment**

**Behavioral performance.** A repeated-measures t-test revealed that behavioral performance on the RB task inside the scanner was consistent with previous behavioral experiments, whereby detection accuracy was reduced on repeat trials relative to nonrepeat trials \( t(22) = 4.72 \), \( P < 0.001 \); see Fig. 2C. In contrast to the behavioral experiments, however, performance on catch trials was significantly above chance [mean 46.4%, SD 5.0%; \( t(22) = 2.67 \), \( P = 0.014 \)], with participants more likely to make erroneous nonrepeat than repeat responses (54.0% vs. 27.1% of errors, respectively; the remaining 19.0% of errors were absent responses). Participants could successfully complete the task blocks on the localizer runs as behavioral performance was close to ceiling (means >93.0%, SDs < 1.2%; \( ts > 36.06 \), \( Ps < 0.001 \) compared with chance).

**Trial types and comparisons.** For the fMRI analyses, we binned repeat and nonrepeat trials into the following conditions: hit (repeat trial, repeat response), miss (repeat trial, nonrepeat response), correct rejection (nonrepeat trial, nonrepeat response), and false alarm (nonrepeat trial, repeat response). Table 2 displays the average response proportions for all conditions. Note that catch trials (or repeat/nonrepeat trials where a ”2 scene only” response or no response was made) were not included in the fMRI analyses because these trials served only as filler trials to reduce the likelihood of guessing responses.

To first isolate the brain areas involved in temporally individuating items during encoding, we compared hit and correct rejection trials, because these conditions place different demands on individuation. That is, given that repeated stimuli presented in close temporal proximity are more difficult to individuate relative to nonrepeated stimuli (Kanwisher 1987), hit trials should, on average, place greater demands on the process of temporal individuation, relative to correct rejection trials. It is important to note that this comparison reflects only trials on which a correct response was made, and we therefore know, with some degree of certainty, that the scenes were successfully individuated in both trial types (although this process was more demanding in under hit trials). In addition, this comparison is balanced in terms of reward associated with making a correct response.

Our second key comparison aimed to identify brain areas involved in the RB deficit (i.e., regions that may underlie the capacity limit on temporal individuation). To do this, we contrasted hit and miss trials, because this comparison reflects instances where two repeated stimuli are successfully detected or not. Because RB reflects an inability to bind a second repeated item’s identity to its token, rather than a failure to create the second token altogether (Kanwisher 1987; Kanwisher et al. 1995; Park and Kanwisher 1994), it was more appropriate to compare between conditions that reflect a misidentification error, rather than trials where participants reported seeing nothing at all (e.g., hits vs. repeated scene/”2 scene only” response trials). Even though this RB comparison uses trial definitions that are based on a postrun selection of trials by accuracy, this is a common approach employed in imaging studies that use RSVP tasks (e.g., Marois et al. 2004). We tested for differences using both univariate gross amplitude and multivariate spatial patterns of BOLD activity.

**Univariate analyses.** For the demands on temporal individuation comparison, we found no significant amplitude differences between hit and correct rejection trials. This finding suggests that the amplitude of activity in all of our ROIs was not modulated by conditions that place differential demands on temporal individuation. On the other hand, when we compared between conditions that reflect a capacity limit of temporal individuation, we found a single region (left hemisphere premotor cortex) that showed significantly greater activity on miss trials relative to hit trials \( t(20) = 3.42 \), \( P = 0.049 \), corrected for multiple comparisons; see Fig. 3). Thus processing in this region may be involved in RB.

### Table 2. Average response proportions to repeat, nonrepeat, and catch trials in the fMRI experiment

<table>
<thead>
<tr>
<th>Trial Type</th>
<th>Repeated</th>
<th>Nonrepeated</th>
<th>Catch</th>
<th>Absent</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Repeat</td>
<td>0.45 (0.11)</td>
<td>0.25 (0.10)</td>
<td>0.05 (0.04)</td>
<td>0.26 (0.13)</td>
<td>1.00</td>
</tr>
<tr>
<td>Nonrepeat</td>
<td>0.14 (0.14)</td>
<td>0.58 (0.15)</td>
<td>0.10 (0.08)</td>
<td>0.18 (0.11)</td>
<td>1.00</td>
</tr>
<tr>
<td>Catch</td>
<td>0.11 (0.09)</td>
<td>0.28 (0.13)</td>
<td>0.46 (0.23)</td>
<td>0.15 (0.10)</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Values are means (SD).
These gross differences in BOLD amplitude were specific to the successful individuation of two repeated stimuli, because none of our ROIs showed any differences in amplitude between correct and incorrect nonrepeated trials (correct rejections vs. false alarms; \( t < 2.16, \text{corrected for multiple comparisons} \ P > 0.0809 \)). This result is consistent with behavioral findings from the lag RB experiment in that it shows that our paradigm specifically taps processing limitations associated with the perception of two repeated stimuli, but not two nonrepeated stimuli (see also Chun 1997). In addition, this difference in amplitude cannot simply reflect response conflict or ambiguity, because this same region responded similarly on hit and false alarm trials (\( t < 1 \)). These trial types showed the greatest difference in reaction time (1,166 vs. 1,430 ms; although response speed was not emphasized in the task) and would arguably reflect the greatest difference in response uncertainty.

**Multivariate analyses.** We further explored the neural underpinnings of temporal individuation and its capacity limits by using ROI-based and whole brain searchlight MVPAs. Because our experimental conditions were jointly determined by stimulus presentation and participants’ responses, the number of trials in each condition was not balanced. Unbalanced trials are particularly problematic for MVPA because this can bias the classifier toward the more numerous condition, rather than the actual properties associated with the experimental conditions (Pereira et al. 2009). To address this issue, we balanced trial numbers across conditions in both training and testing subsets by removing a random selection of trials from the more plentiful condition before the MVPA. Decoding results for the ROI-based MVPA were averaged across 100 repetitions of this procedure, and the number of iterations was reduced to 10 for the searchlight analysis to save computation time. With the use of this strict balancing method, there was an average of 35 trials in training sets and 5 trials in testing sets in each cross-validation loop.

**ROI-based MVPAs.** To first identify differences in activity patterns associated with the demands placed on temporal individuation, we trained a classifier to discriminate between hit and correct rejection trials in each of our ROIs. Above-chance decoding performance for this comparison emerged in 17 of our 18 ROIs (\( t > 4.22, P < 0.01, \text{corrected for multiple comparisons} \)); see Fig. 4. Although activity in the left hemisphere dorsolateral prefrontal cortex (DLPFC) could be discriminated between these two conditions for the 21-mm ROI cube, this result did not hold for the 15-mm ROI cube \( [t(18) = 2.28, P = 0.637] \). The significant ROIs included both lower-level areas involved in perceptual processes (e.g., Epstein et al. 2003; Kourtzi and Kanwisher 2001; Xu 2009) and higher-level executive areas that have previously been associated with other capacity-limited processes, such as response selection, decision making, and encoding (e.g., Dux et al. 2006, 2009; Heekeren et al. 2004; Szameit et al. 2002; Tombu et al. 2011). In contrast, the classifier was only able to differentiate between activity patterns associated with successful and unsuccessful instances of temporal individuation (hits vs. misses) in the left hemisphere superior IPS/SPL \( [t(21) = 3.58, P = 0.031, \text{corrected for multiple comparisons}] \). This result, however, did not hold over changes in ROI size (classification under 15-mm ROI cube, corrected for multiple comparisons \( P > 1 \)). These multivariate results therefore suggest that perceptual demands placed on temporal individuation influence the patterns of activity across a widely distributed set of brain regions, including both lower and higher cortical areas. This finding contrasts with the single brain region that has previously been associated with spatial individuation (Xu 2009) in that it suggests that this process is underpinned by a far more distributed set of areas.

**Control analyses.** We conducted an additional set of control MVPAs to test whether the distributed differences in activity patterns associated with hit and correct rejection trials were driven by other differences that existed between these conditions (i.e., not related to individuation). Because hit and correct rejection trials showed significant differences in reaction time \([1,166 \text{ vs. } 1,297 \text{ ms}; t(22) = 4.23, P < 0.001] \), the first control analysis aimed to assess whether our results could be attributed to task-related effects such as general difficulty or the amount of time spent on the task. Using reaction time as a proxy for task difficulty, we trained classifiers to discriminate between the two trial types that showed the largest difference in reaction time: hit (1,166 ms) and false alarm (1,430 ms) trials \( [t(22) = 5.50, P < 0.001] \). Significant decoding emerged for this comparison in the anterior cingulate cortex (ACC) and right hemisphere LOC (\( t > 3.46, P < 0.042, \text{corrected for multiple comparisons} \)); however, only the ACC result was also observed for the 15-mm cube \( [\text{ACC}; t(21) = 3.94, P = 0.014; \text{right hemisphere LOC}; t(21) = 2.96, P = 0.134] \). Results from this control analysis suggest that, with the possible exception of the ACC, the distributed patterns of activity associated with the perceptual demands placed on temporal individuation do not simply reflect task difficulty or the amount of time spent on the task. In contrast to the remaining ROIs, the activity patterns in the ACC likely reflect general task difficulty as opposed to a specific difficulty associated with individuating two scenes. Furthermore, the lack of significant results are unlikely to reflect insufficient power due to the low number of false alarm trials, because our results from the demands on temporal individuation comparison held for all previously significant ROIs (\( t > 3.29, P = 0.078 \) for left hemisphere inferior frontal junction; \( t > 3.48, P < 0.048 \) for all other ROIs, both corrected for multiple comparisons) even when we equated trial numbers across all trial types, rather than only across the conditions being compared.

The second set of control analyses tested whether the differences in activity patterns associated with temporal individuation reflected purely stimulus- or response-related effects, since hit and correct rejection conditions differed on both these factors. To first test for stimulus-related differences in activity, we decoded patterns of activity associated with repeated and nonrepeated stimuli, regardless of participants’ responses. For this analysis, we collapsed across both repeated stimulus (hits and misses) and nonrepeated stimulus conditions (correct rejections and false alarms) to give ourselves the best chance of detecting any stimulus-related effects if they did indeed exist. Because we used all four trial types in this analysis, we balanced trial numbers across all conditions before decoding to ensure the differences in trial numbers did not affect the results. No significant decoding emerged between repeated and nonrepeated stimulus conditions in any region \( [t < 2.97, P > 0.126, \text{corrected for multiple comparisons}; \text{see Fig. 5}] \), suggest-
ing that none of our ROIs exclusively coded for stimulus properties in this experiment.

We also decoded activity patterns associated with repeated and nonrepeated responses regardless of the stimulus presentation (hits and false alarms vs. misses and correct rejections) and found these two conditions could be discriminated in 2 of the 18 ROIs: the right hemisphere PPA and left hemisphere sIPS/SPL ($t > 3.38$, $P = 0.048$, corrected; see Fig. 5). The same decoding performance in these regions did not hold across both ROI sizes, however, suggesting that the response coding in these regions was not reliable ($t < 2.80$, $P = 0.189$ for 15-mm ROI cube). Thus the widespread differences in patterns of activity associated with hit and correct rejection conditions did not appear to be purely stimulus or response based, but rather reflected an interaction between these stimulus and decision/response factors that would be necessary to individuate temporally distinct items.

Although our results were not driven by stimulus and response factors individually, one could argue that they reflect a simple stimulus-response interaction, rather than anything specific to temporal individuation. To provide further support that our hit vs. correct rejection comparison reflects temporal individuation demands, rather than some other sort of stimulus-response interaction, we decoded miss vs. false alarm trials (we balanced trial numbers in this comparison as well, like all other analyses). These are both incorrect trials, so we cannot be sure of the extent to which each critical item was individuated, but these trials do differ in terms of the stimulus presented and the response made. Unlike our key analysis of hit vs. correct rejection, the analysis of miss vs. false alarm revealed significant decoding in the bilateral LOC only ($t > 3.49$, $P = 0.039$, corrected). Importantly, after averaging over decoding values in all the ROIs, to increase statistical power and counter the fact that not all subjects showed every ROI (see Table 1), we found that the overall decoding across the brain for hits vs. correct rejections was significantly greater than that found for misses vs. false alarms [$t(22) = 2.91$, $P = 0.008$, uncorrected because data were averaged across all ROIs]. Collectively,
these results suggest all significant hit vs. correct rejection ROIs, with the possible exception of the bilateral LOC, reflect the specific stimulus-response interaction involved in temporal individuation. As we elaborate on in the DISCUSSION, we propose that such interactions are facilitated within a distributed neural framework or “workspace” in which information can be shared between lower and higher regions (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004).

A final control analysis was conducted to ensure that results from the demands on temporal individuation analysis did not simply reflect a data artifact that would produce above chance decoding across the entire brain. To test this, we decoded activity patterns in two additional control ROIs that predominantly respond to auditory information rather than visual information (left and right primary auditory cortices). These ROIs were anatomically defined as the superior region of the temporal lobe (Rademacher et al. 2001). We decoded activity in these areas for the two main comparisons and the task difficulty control comparison. If decoding performance in the temporal individuation analysis did indeed reflect the differential perceptual demands associated with individuating visual stimuli across time (and not an artifact in the data, task design, or analysis), the classifier should be no better than chance at discriminating between hit and correct rejection conditions in either of these control regions. Consistent with this prediction, no significant decoding emerged in either of the auditory ROIs for any of the classifier comparisons, including the demands on temporal individuation comparison ($t_{11021}/H = 2.32, P_{11022} = 0.044, \text{corrected for multiple comparisons}; \text{Fig. 6}$).

Searchlight analysis. We conducted a whole brain searchlight analysis to determine if brain regions other than our ROIs could discriminate between the different demands placed on temporal individuation. Consistent with our previous ROI-based MVPA, the searchlight analysis revealed that widespread parts of the brain show distinct activity patterns for hit compared with correct rejection trials (Fig. 7). The information map generated from this analysis included all of our ROIs and provided confirmatory support for the findings that emerged in

![Fig. 5. Results from the stimulus and response multivariate control analyses. Format is the same as Fig. 4. To identify purely stimulus-driven changes in activity patterns, we compared repeated and non-repeated stimuli trials, regardless of participants' responses (hit and miss vs. CR and FA; open bars). Likewise, to isolate purely response-driven changes in activity patterns, we contrasted instances where participants made a repeated and nonrepeated response, regardless of the stimulus presentation (hit and FA vs. CR and miss; solid bars).]
our ROI-based MVPA. In addition to these ROIs, we also found that large parts of the frontal, parietal, and occipital cortices were sensitive to the conditions under which temporal individuation occurred. Consistent with our control ROI analysis, no voxels in the auditory cortices could be reliably classified, suggesting that our classification results do not reflect an artifact of the data analyses. We also performed a searchlight analysis for the RB comparison but found no significant classification across the entire brain. This finding further supports the idea that the processing limitations that lead to RB modulate the amplitude, rather than the patterns, of BOLD activity.

DISCUSSION

The purpose of the present study was twofold. First, we aimed to examine whether individuation processes could be localized to a single neural correlate or if this operation tapped a widely distributed network of brain areas, as has been proposed in models of consciousness and encoding (Baars and Franklin 2003; Dehaene et al. 2003; Sergent and Dehaene 2004). Second, we aimed to pinpoint the neural areas involved in the behavioral RB deficit. To accomplish these goals, we employed an RB paradigm and a combination of univariate and multivariate analysis techniques. In response to the first aim, we found that activity patterns associated with the perception of two repeated stimuli (which are more demanding to individuate) and nonrepeated stimuli (which are relatively easy to individuate) could be successfully discriminated. Critically, these two conditions reflected correct trials, meaning that we can be confident that stimuli were successfully individuated on these trials, although this process was more demanding for repeated stimuli. Even though these two conditions could not be distinguished when univariate BOLD amplitude was compared, our multivariate analyses revealed that these conditions elicited reliably different spatial patterns of activity in the majority of our ROIs. This set of regions included both lower-level perceptual and higher-level attentional/executive regions that covered parts of the frontal, parietal, and occipital cortices. Although we cannot be sure of the stage(s) of processing at which the increased demands associated with temporal individuation had their impact, our findings nevertheless demonstrate a measurable difference in BOLD activity that is evoked by these changes in temporal individuation demands.

For our secondary analysis, to identify the brain area(s) associated with RB (i.e., a processing limitation associated with temporal individuation), we compared activity between conditions in which two repeated stimuli were successfully detected or not. In contrast to the primary analysis in which we manipulated the demands on temporal individuation, we found that this RB analysis did not reliably affect the spatial patterns of activity in any of our ROIs, but instead modulated the amplitude of BOLD activity in the left hemisphere premotor cortex. Together, our findings suggest that a large group of
cortical regions are sensitive to demands placed on the temporal individuation process, whereas the processing limitations associated with this operation that lead to RB specifically influence the strength of activity in a focal brain region. Our two key comparisons therefore appear to reflect distinct processes: the demand or load associated with constructing an individuated representation across time, and a specific capacity limitation associated with individuation.

The differences that emerged for the amplitude and patterns of BOLD activity resonate with recent findings in the visual short-term memory literature. Several studies have shown that increasing the number of items held in memory leads to sustained, elevated BOLD amplitude in the parietal cortex (Todd and Marois 2004; Xu and Chun 2006), yet maintaining these items in memory alters the patterns, but not the amplitude, of activity in early sensory areas (e.g., Emrich et al. 2013; Serences et al. 2009). Emrich et al. (2013) suggest that changes in activity patterns in sensory areas reflect the precision of item representations (see also Ester et al. 2013), whereas changes in amplitude are associated with the allocation of attention resources to a limited number of items. An analogous explanation fits our findings, where the distributed changes in activity patterns associated with the demands placed on temporal individuation could reflect the precision of individuated representations, whereas the specific changes in amplitude reflected by RB could arise from processing limitations associated with the allocation of attentional resources that are necessary to bind an individuated representation (token) to its identity (type).

Decoding associated with the demands placed on temporal individuation was only attributed to a general effect of task difficulty in one ROI (the ACC), because the patterns of activity in the remaining ROIs did not discriminate between differences in reaction time. These remaining regions appear to reflect the demands associated with individuating two temporally distinct scenes, whereas the ACC appears to code for more general task-related effects. This latter finding fits well with the existing literature that suggests that the ACC is involved in general task conflict and cognitive control (Kerns et al. 2004).

Differences associated with temporal individuation were also distinguished from purely stimulus- or response-related effects, because classifiers could not consistently discriminate between repeated and nonrepeated stimuli (regardless of participants’ responses) or responses (regardless of the physical stimulus presentation) in any of our “temporal individuation” regions. This finding suggests that these brain areas code for the interaction between stimulus and decision/response factors associated with successfully individuating two temporally distinct visual items. Of import, this stimulus-response interaction appears to be specifically related to temporal individuation in all regions with the possible exception of the bilateral LOC, since it was only in this area where patterns of activity could distinguish between miss and false alarm trials. These trials differ in stimulus and response characteristics but likely do not differ in the demands they place on temporal individuation. Moreover, when we collapsed decoding results across all ROIs for the hit vs. correct rejection comparison and miss vs. false alarm comparison, we found a significant overall difference between these two comparisons, suggesting that the information reflected by these two comparisons differs across the brain. In addition, signals associated with hits and correct rejections were restricted to brain regions that code for visual information or higher-level abstractions that do not depend on perceptual modality, and our decoding findings did not extend to other nonvisual (auditory) areas. Thus activity patterns associated with the differential demands placed on temporal individuation did not merely reflect false positives across the entire brain. Finally, our key individuation results cannot reflect general positive effects of target detection (e.g., reward, satisfaction), because both hits and correct rejections represent correct trials and would presumably have elicited the same level of reward and satisfaction.

In contrast to the wide set of brain areas that emerged in the current study, previous research and theoretical models of object individuation have attributed this operation to a single brain region (see Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007, 2009). Studies such as those by Xu and colleagues are common in cognitive neuroscience literature and assume that any given perceptual or cognitive process will be supported by a focal set of brain areas. Although this approach is hypothesis driven, it can be problematic as it limits the underlying neural substrates associated with particular processes and might miss the involvement of a more diffuse network of brain regions (see Vickery et al. 2011). For example, it was previously thought that signals associated with reward processes were represented in specific parts of the basal ganglia and prefrontal and parietal cortex (Elliott et al. 2000; Kable and Glimcher 2007; Kahn et al. 2010; Rushworth and Behrens 2008; Vickery and Jiang 2009). More recently, however, Vickery et al. (2011) used MVPA to show that reward processes are reflected across the whole brain, suggesting that cognitive operations (such as temporal individuation, studied here) can be underpinned by an extensive neural network. Interestingly, these authors identified only a small subset of areas involved in reward processing when employing a univariate approach.

The widespread patterns of activity that emerged for temporal individuation are instead in line with existing accounts of consciousness, such as the “global neuronal workspace” model (Dehaene et al. 2003; Sergent and Dehaene 2004; see also Baars and Franklin 2003). According to this framework, conscious awareness is underpinned by a distributed network of “workspace neurons” that communicate via long-range connections in the brain. For a stimulus to be consciously perceived, it must activate this workspace, which then allows information to be accessed by a wide variety of processes. The global neuronal workspace model hypothesizes that these neurons are present in both early sensory areas and higher-level parietal and frontal areas, and information about a given stimulus is transferred through recurrent communications between different levels of the cortical hierarchy. In the context of the present study, these long-range connections provide a possible avenue in which lower and higher cortical areas interact during temporal individuation. We hypothesize that conditions in which it is more demanding to individuate two distinct object occurrences alter communications within this distributed workspace, leading to changes in the resulting patterns of activity in both lower- and higher-level brain areas. Our findings provide important insights into the neural underpinnings of temporal individuation in that we show it is a far more distributed process in the brain than initially proposed (e.g., Xu 2009; Xu and Chun 2009).
It is interesting to consider the discrepancy between the results we report presently and those from prior investigations into individuation by Xu and colleagues (Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007). These previous studies implicated the inferior IPS as the sole substrate of object individuation, which contrasts with the more diffuse group of brain regions we found in the current work. Even when we analyzed our data using the same univariate method as Xu and colleagues, we found that BOLD activity in a smaller group of ROIs was modulated by the demands placed on temporal individuation (ACC and superior medial frontal cortex, left hemisphere DLPFC and left hemisphere LOC, ts > 2.18, Ps < .043, using the uncorrected test as in Xu and colleagues), but this subset did not include the inferior IPS. Below we consider several key differences between these previous studies and our work that could account for this discrepancy.

First is the episodic context in which object individuation was investigated. In our paradigm, items could only be individuated using temporal cues, whereas participants in Xu and colleagues’ studies could only rely on the items’ spatial locations (see Jeong and Xu 2013; Xu 2009; Xu and Chun 2006, 2007). It is unknown how the neural mechanisms associated with object individuation processes differ between the spatial and temporal domains, and the types of paradigms used in these studies and the present study are too dissimilar to make any strong conclusions regarding how these two operations might be related. Further research using a single paradigm that can manipulate spatial and temporal individuation processes will be useful in informing us about the nature of these two processes in the brain. Second, Xu and colleagues examined a different aspect of object individuation from the present study. In the present study we looked at the brain areas that support the process of individuation during perception, whereas Xu and colleagues’ investigations focused on how individuated representations are consolidated, stored, and retrieved in visual short-term memory. An interesting possibility could be that different groups of brain areas are recruited when individuated representations are constructed during perception and later stored in memory.

Could the neural operation associated with temporal individuation simply reflect other forms of repetition processing in the brain? Repetition suppression, for instance, is a phenomenon wherein the presentation of a repeated stimulus leads to a reduction in neural activity (Desimone 1996; Grill-Spector et al. 2006; Henson and Rugg 2003; MacKay and Miller 1994). Like the distributed signals that emerged in response to the differential demands placed on temporal individuation, repetition suppression has also been detected extensively throughout the brain (Gotts et al. 2012). Our findings are unlikely to reflect repetition suppression for two key reasons, one reflecting methodology and the other a control analysis. First, the differential patterns of activity we observed for successfully individuating repeated and nonrepeated stimuli were present after gross differences in mean BOLD amplitude were removed from each condition. Thus the activity patterns that emerged for temporal individuation specifically reflect differences in spatial patterns of activity, not gross amplitude. Second, we were unable to decode purely stimulus-related changes in activity patterns associated with repeated and nonrepeated stimuli (hits and misses vs. correct rejections and false alarms) in any ROI. Rather, the regions that could discriminate between hits and correct rejections appear to be sensitive to the conditions under which the correct perceptual representation is successfully registered for a given stimulus. Our findings can therefore be distinguished from repetition suppression effects in the brain.

The present study also provides novel behavioral and fMRI evidence regarding the locus of RB. Although RB has been demonstrated for a variety of simple and complex stimuli (see, for a review, Coltheart 2010), our behavioral findings extend the generality of RB by providing the first evidence that this deficit can occur for the perception of scenes. In addition, our univariate fMRI results provide new insights into the ongoing debate over whether RB reflects an early (Kanwisher 1987; Luo and Caramazza 1996) or late (Fagot and Pashler 1995; Whittlesea and Masson 2005) processing locus. Although the limited electrophysiological investigations into RB suggest that this deficit arises between 220 and 350 ms after the repeated stimulus appears (Koivisto and Revonsuo 2008; Schendan et al. 1997), the paradigms used in these studies do not exclusively tap the capacity limits of individuation. To our knowledge, this study reflects the first neuroimaging work conducted using RB, where we found that the gross amplitude of BOLD activity in a higher-level premotor area involved in processes such as top-down attention and response selection (e.g., Marois et al. 2006; Schumacher et al. 2003) was influenced by whether participants successfully detected two repeated stimuli or not. Contrary to the prominent models of RB, this result suggests that this deficit has neither a purely perceptual or memory retrieval locus but reflects a mid-level top-down attentional bottleneck in conscious awareness (see also Chun 1997).

The direction of amplitude differences for the capacity limits of temporal individuation might appear counter to what one would predict, because activity in the left hemisphere premotor cortex was increased when a repetition was missed, compared with when it was correctly detected. Similar findings were noted in the AB literature, however, such that activity in two occipitotemporal regions were enhanced when two different letters were missed, relative to when they were detected (Kranzioch et al. 2005). Because RB is hypothesized to reflect an inability to bind an individuated token to a repeated type (Kanwisher 1987; Park and Kanwisher 1994), the enhanced activity associated with miss trials could reflect maintenance of the second target’s type representation as the visual system attempts (but is unable) to register the source of this representation. Similar to Kanwisher’s original type-token account (Kanwisher 1987; Park and Kanwisher 1994), this interpretation suggests that the increased activation that emerged for miss trials, relative to hit trials, reflects changes in processing of the second target rather than the first.

The present findings also add to the existing literature on the relationship between RB and other capacity-limited processes such as the AB. Behavioral comparisons between these two phenomena have found similar results to our lag RB experiment, in that they suggest that the AB and RB reflect distinct processing limitations (Chun 1997; Dux and Marois 2007). This apparent dissociation is further supported by the present fMRI findings, because we found different regions were implicated in RB relative to the AB, which has been associated with activity in parts of the lateral frontal, posterior parietal and occipitotemporal cortices (Kranzioch et al. 2005; Marcantoni...
et al. 2003; Marois et al. 2004). Although we are limited in making strong conclusions about the possible neural dissociation between the AB and RB given that these investigations differed in paradigm and task, these findings do suggest that these two phenomena might be dissociable neurally as well as behaviorally. Our findings point towards the possibility of exploring the dissociation or overlap in the brain between different bottlenecks in conscious awareness.

We have provided the first evidence for an extensive set of brain regions that support the process of temporal individuation in perception, as well as the neural consequences associated with the processing limitations that lead to the RB deficit. We found that varying the demands placed on temporal individuation produced distributed changes in the patterns of activity across the brain, suggesting that such processes operate within a widespread neuronal workspace and involve multiple sources of information (e.g., stimulus, decisional, response). In contrast, when the capacity limit of individuation is reached, there are focal increases in the gross amplitude of BOLD activity, possibly reflecting changes in the allocation of attentional resources to processing the second repeated target. These findings highlight apparent differences in the neural coding of two distinct processes associated with temporal individuation, namely, the demands under which individuated representations are generated and the capacity limits that bottleneck the binding of these individuated tokens to an identity representation for conscious report.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS


REFERENCES


