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Selective biasing of a specific bistable-figure percept involves fMRI signal changes in frontostriatal circuits:

A step toward unlocking the neural correlates of top-down control and self-regulation

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Abstract

Attention, suggestion, context and expectation can all exert top-down influence on bottom-up processes (e.g., stimulus-driven mechanisms). Identifying the functional neuroanatomy that subserves top-down influences on sensory information processing can unlock the neural substrates of how suggestion can modulate behavior. Using functional magnetic resonance imaging (fMRI), we scanned 10 healthy participants (five men) viewing five bistable figures. Participants received a directional cue to perceive a particular spatial orientation a few seconds before the bistable figure appeared. After presentation, participants pressed a button to indicate their locking into the one desired orientation of the two possible interpretations. Participants additionally performed tests of impulse control and sustained attention. Our findings reveal the role of specific frontostriatal structures in selecting a particular orientation for bistable figures, including dorsolateral prefrontal regions and the putamen. Additional contrasts further bolstered the role of the frontostriatal system in the top-down processing of competing visual perceptions. Separate correlations of behavioral variables with fMRI activations support the idea that the frontostriatal system may mediate attentional control when selecting among competing visual perceptions. These results may generalize to other psychological functions. With special relevance to clinical neuroscience and applications involving attention, expectation and suggestion (e.g., hypnosis), our results address the importance of frontostriatal circuitry in behavioral modulation.

Keywords

Top-down effect; cognitive control; cortico-striato-thalamocortical (CSTC) circuits; attention; expectation; hypnosis; self-regulation; impulse control

Multiple experiments have demonstrated that attention, expectation and hypnosis may influence information processing in the human brain (Kosslyn, Thompson, Costantini-

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¹The ability to manipulate one's own emotions, thoughts, or actions upon direction from the self or another person. Emotion regulation can be a form of self-regulation, but it could also be induced by a caregiver's actions.

²The reduction in the probability, speed, or vigor of the normal response to a stimulus based upon instruction from the self or other. It is often measured by scale scores on a questionnaire or by a task that requires one to withhold or delay a response.

³The literature typically uses the appellation "emotional-regulation" to mean the reduction, increase, or sustaining of an emotional response (e.g., fear, anger, or pleasure) based upon the actions of the self or another.

⁴The ability to inhibit, activate or sustain a response, including the capacity to inhibit a dominant response in order to perform a subdominant response. In temperament research individual differences in effortful control are measured as a factor score that combines scales dealing with attention and the ability to regulate behavior on command.

Ferrando, Alpert, & Spiegel, 2000; Raz, 2004b; Raz & Buhle, 2006; Raz, Fan, & Posner, 2005; Raz et al., 2003b; Raz, Shapiro, Fan, & Posner, 2002; Wager et al., 2004). Both endogenous, top-down control, and exogenous, bottom-up capture of attention, enhance performance by affecting relative increases in neural activity in a given sensory system (Raz & Buhle, 2006). The ability to use higher brain functions to influence downstream processing draws on the neural substrates that are often explored in the study of volitional agency, effortful control, and consciousness (Baumeister & Vohs, 2004; Churchland, 2002; Koch, 2004; Posner, 2004a; Wegner, 2002). Defining the functional anatomy that subserves these top-down influences will likely elucidate how we can shape our reality by formulating perceptions, regulating thought and action, and experiencing the external world according to preexisting conceptual schemas (Raz, Marinoff, Zephrani, Schweizer, & Posner, 2004; Raz & Shapiro, 2002; Raz, Zephrani, Schweizer, & Marinoff, 2004). Unlocking the brain mechanisms underlying such effects is paramount to unraveling the power of clinical therapies drawing on such phenomena as attention and hypnosis (Raz, 2005). One way to examine such top-down effects in the laboratory exploits the visual characteristics of bistable figures (BFs) (Long & Toppino, 2004).

BFs are planar images that are alternately identifiable as one of two disparate percepts (Gregory, 1997). BFs can be used to distinguish elementary sensory features of the physical image from the top-down processes involved in construing either of its visuospatial interpretations (Long & Toppino, 2004). For example, the Necker cube can be perceived (i.e., sensed and interpreted) as either facing upward and to the left or downward and to the right (Figure 1A). Individuals show less attentional control of alternation rates for the Necker cube than for BFs that have multiple object interpretations (e.g., duck/rabbit, chef/dog) (Struber & Stadler, 1999). If naive observers can selectively bias Necker cube reversal, it seems reasonable to expect that attentional control in highly practiced observers would likely be effective for other such BFs. In this paper, we explore whether this potential generalizability of attentional self-regulation may lend itself to clinical applications, especially those involving suggestion and expectation including hypnosis.

Perceptual rivalry consists of fluctuations in visual perception despite unchanging visual input, unlike binocular rivalry which is more specific in that the two competing interpretations correspond to images projected on each of the two eyes. Nonetheless, both offer a means for understanding the relationship between top-down effects and perceptual information. A common theme in early models of binocular rivalry explains the phenomenon of selecting a specific visuospatial interpretation of BFs as reciprocal inhibition that occurs as early as at the retinal level of information processing (Blake, 1989). However, with growing recognition that attention can bias the activity of neuronal populations (Posner, 2004a) and that patients with attentional deficits can display difficulty in switching from one percept to another when viewing BFs (Wilkins, Shallice, & McCarthy, 1987), the role of attentional mechanisms has become more evident. Indeed, interpretations of recent functional magnetic resonance imaging (fMRI) data suggest that certain attentional processes drive switching between competing visuospatial orientations (Logothetis, Leopold, & Sheinberg, 1996; Tong & Engel, 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Thus, attention affects perception (Raz, Marinoff, Zephrani, Schweizer, & Posner, 2004; Raz, Zephrani, Schweizer, & Marinoff, 2004).

Neuroimaging studies have revealed the ways in which separate brain areas orchestrate attention for the regulation not only of binocular rivalry and perception, but also of conflict and affect (Bush, Luu, & Posner, 2000; Lamar, Yousem, & Resnick, 2004; B. S. Peterson et al., 2002; Posner & Rothbart, 1998; Rothbart, Ellis, & Posner, 2004; Rothbart, Ellis, Rueda, & Posner, 2003). Investigations of top-down control have been extended to psychopathologies that putatively involve impaired self-regulation (e.g., Tourette's syndrome, Bipolar Disorder, and Attention-Deficit/Hyperactivity Disorder) (Blumberg et al., 2003; B. S. Peterson et al.,

1998; B. S. Peterson & Thomas, 2000). These conceptual formulations collectively suggest that in addition to dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC), a key network for behavioral inhibition resides within cortico-striatothalamo-cortical (CSTC) circuits (B. S. Peterson et al., 2002; A. L. Spessot, Plessen, & Peterson, 2004). Because CSTC circuits, particularly projections from frontal cortices to the basal ganglia, are involved in inhibitory control, attentional regulation, and sensory modulation (Casey et al., 1997; Casey et al., 2000; Hayes, Davidson, Keele, & Rafal, 1998; Tekin & Cummings, 2002; van den Heuvel et al., 2003), we hypothesized that these circuits would be active when forcing a specific visuospatial interpretation of BFs. We tested this hypothesis using fMRI and correlated task-dependent brain activity to independent measures of attentional control and task difficulty.

Methods

Participants

Five men (26.1±2.9 years old) and five women (24.8±3.0 years old) were recruited from the local community. Six were Caucasian, one was African-American, and three were Asian-Americans. All participants except one were right-handed, and all were without a history of neurological problems, Axis I psychiatric disorders, or head injury. On average, participants were in the high range for estimated IQ (115±8.1) based on the Wechsler Abbreviated Scale of Intelligence (WASr) (Wechsler, 1999). Participants were representative of young healthy controls and provided written informed consent in compliance with the local institutional review board.

BF Training and Rating

We used five bistable geometric forms (Card, Mach Pyramid, Necker Cube, 3-D Triangle, and Wave; Figure 1A-E). BFs in the current study were designed to control for basic stimulus features, semantic properties in each of the orientations, and cognitive associations to the stimulus. Upon first viewing the BFs, out of the scanner, participants rated each on both selection and maintenance using a Likert scale ranging from 1 to 5 (1 representing the easiest and 5 the most difficult). A brief questionnaire also assessed which orientation (FRONT, BACK, or no preference) was easier or more difficult to select and maintain, thus identifying “easy” and “difficult” BF orientations, respectively. Finally, participants indicated the 3D orientation in which they initially perceived each figure (i.e., whether their original perception was FRONT, BACK, or no preference). Nine out of 10 participants completed the questionnaire.

Next, participants trained outside the scanner until they reported proficiency in selecting and maintaining a specific orientation; participants practiced selecting and maintaining each BF in both the FRONT and BACK orientations. Although bottom-up factors such as fixation position can bias BF perception (Einhauser, Martin, & König, 2004), previous studies have shown these effects to be relatively small (Kawabata, Yamagami, & Noaki, 1978; Toppino, 2003). Nonetheless, to minimize eye movement, which may influence the orientation to be perceived in addition to how rapidly spontaneous alternations occur, participants were required to fixate on a point embedded within the BF while an experimenter closely monitored their eye movements and provided verbal feedback throughout training. Only when participants reported the ability to volitionally select and maintain a BF orientation for at least 20 seconds in the absence of observable eye movements, were they deemed proficient. This training process took about 20 minutes.

BF Scanning

As depicted in Figure 1F, the sequence of stimulus presentation for each BF was as follows: a unitary fixation point appeared on the screen for the first 10.5 seconds. This fixation point

remained in the same position for all ensuing stimuli throughout the entire run. Then, a directional cue (either FRONT or BACK) appeared on the screen for 3 seconds above the fixation point, indicating how participants were to construe the imminent BF. At 13.5 seconds, the BF embedding the fixation point appeared on the screen and remained on display for 40 seconds. The figure then disappeared, leaving only the fixation point. Each stimulus was presented twice during the scan session, once for each of the two designated orientations (FRONT or BACK). The order of the stimulus presentation was pseudorandomized within and across all runs. Participants were instructed to press a button with their right index finger when the cued perceptual orientation of the displayed bistable figure stabilized in their mind. The duration between figure onset and the first button press thereafter was designated the "SELECTION" epoch of the fMRI time series. Participants were instructed to press the button a second time if their visual interpretation changed before the end of the trial. The duration between the first button press and either a second button press or the termination of the trial, whichever came first, was designated as the "MAINTENANCE" epoch. Total time per run was 8 minutes and 42 seconds. Whereas six runs were acquired for 9 participants, five runs were acquired for 1 subject due to a technical problem with one of the runs.

Stimulus Presentation

Stimuli were presented in white ink against a black background, back-projected onto a screen positioned in front of the subject at the opening of the magnet's bore. Participants viewed the display through a double-sided mirror mounted above the head coil. Nearsighted participants were fitted with prescription lenses to view the screen clearly. All Stimuli were presented using the PS YSCOPE software (Cohen, MacWhinney, Flatt, & Provost, 1993) running on a G3 Macintosh computer (Apple Computer, Cupertino, CA). A digital interface enabled the Macintosh to record the time of acquisition of each image, enabling precise synchronization of stimulus presentation with image acquisition (within 20 msec). BFs subtended 4 vertical and 4 horizontal degrees of the visual field.

Additional Tasks Performed Outside the Scanner Stroop Color-Word Interference Test

The Stroop effect is an index of response inhibition (Lezak, 1995). Two tasks, A and B, were administered. Task A required participants to name the color of 126 red, green, or blue dots arranged randomly in a 9×14 matrix. In task B, participants were asked to name the color of a similar array of words written in incongruent colors (e.g., "red" printed in blue ink). Participants were instructed to work as quickly as they could, as time to completion was recorded. Stroop Interference was calculated as a difference score, Task B - Task A (Jensen, 1965). This variable was used as a covariate in a regression analysis with the magnitude of fMRI signal changes.

Connors' Continuous Performance Test - second Edition (CPT-II)

The CPT-II is a measure of motor inhibitory control (Connors, 1994). Participants respond with a button press to all targets except for the target letter. Thus, the motor system is primed to respond, and for a small number of (he trials, the subject is required to inhibit the prepotent response. CPT-II is sensitive to errors of impulse control and dysfunctions of sustained attention. Commission errors measured impulsivity and self-regulation, whereas an additional score (d') measured attentiveness. These variables were used as covariates in separate regression analyses with fMRI signal changes.

MRI Scanning

The present study used the neuroimaging technology known as fMRI - a non-invasive technique that permits imaging of the living brain and provides findings that relate neural to cognitive activity by measuring small changes in the magnetic properties of blood. Imaging

was performed on a General Electric 1.5 T Signa LX scanner (Milwaukee, WI). Head positioning in the magnet was standardized using canthomeatal landmarks. AT1-weighted sagittal localizing scan was used to position the axial images. In all participants, 16 axial T1-weighted slices were acquired, oriented parallel to the anterior commissure/posterior commissure (AC-PC) line, with 9 slices positioned above the AC-PC line, one inclusive of it, and 6 below. Slice thickness was a constant 7 mm, while the skip between slices varied between 0.5 mm and 2.0 mm to position each axial slice at the same axial location across participants as the corresponding axial sections of the Talairach coordinate system (Talairach & Tournoux, 1988). Functional images were acquired at the same locations as the 16 axial T1-weighted slices using a gradient-recalled, single shot, echoplanar pulse sequence with 348 images per slice. Time to Repetition = 1500 ms, Time to Echo=60 ms, Flip Angle=60°, Matrix 64 × 64, Field of View=20 × 20 cm, slice thickness=7 mm, in-plane resolution of 3.125×3.125 mm

Image Preprocessing

Studies were visually inspected for ghosting artifacts. SPM99 (Wellcome Department of Imaging Neuroscience, University College, London) was then used to motion-correct the echoplanar images across all runs, with realignment registered to the first image of the first run. Images were discarded if peak motion estimates exceeded a 1.5 mm displacement or 2° of rotation. The T1-weighted axial images were coregistered to the axial echoplanar images using the mutual information coregistration option of SPM99. The T1-weighted axial images were then spatially normalized to the SPM99 T1-weighted image template, the Montreal standardized atlas. These same normalization parameters were used to reformat the axial echoplanar images, which were then reformatted to 2×2×2 mm isotropic voxels and spatially smoothed using an 8-mm full-width-half-maximum (FWHM) Gaussian kernel to reduce noise and to help ensure the validity of analyses across participants. Image intensities were globally normalized to correct for intensities within each run. Low-frequency components of the fMRI time series were removed using a high-pass filter, calculated as two times the longest interval between two appearances of the most frequently occurring event. We temporally smoothed the images with a Gaussian filter with length of 4s to remove high-frequency noise below the limits of temporal resolution determined by the hemodynamic response function.

Analysis of fMRI Data

Statistical analyses of the fMRI data were performed using SPM99 (Wellcome Department of Imaging Neuroscience, University College, London). Onset times of each event type (10-second gaze fixation, 3-second directional cue and each BF presentation, a 1.5-second button press, and a variable MAINTENANCE period) were entered into the design matrix and then convolved with the canonical hemodynamic response function.

The task was initially analyzed for each subject individually before inclusion in multi-subject analyses using the general linear model of SPM99. Thus, individual contrast images were created for each subject within each condition. Each subject's contrast images were intensity-normalized using the respective last beta images in the fMRI time series to standardize image intensity across all runs of a scanning session. A conjunction mask was applied to these individual contrast images to ensure that only voxels without signal voids for all individuals were analyzed. The resulting images were smoothed using an 8 mm FWHM Gaussian kernel.

These spatially smoothed images were entered into a random effects analysis to eliminate highly discrepant variances between and within participants in constructing appropriate error terms for hypothesis testing, as well as to permit generalizability to the population (Friston, Holmes, Price, Buchel, & Worsley, 1999; Friston, Holmes, & Worsley, 1999). The multi-subject group analysis requires input of one scan per subject for each condition within a mixed-

model analysis to account for both random effects (of the scan) and fixed effects (of task condition). The statistical contrast of interest was SELECTION versus gaze FIXATION. This contrast assessed the selection of one competing visual perception over another while attempting to control for aspects of attention and eye movement. To help protect against false positives due to multiple statistical comparisons within voxels, we invoked a threshold of p -values ≤ 0.001 with a spatial extent of 4 voxels for activation (F -maps) (Friston et al., 1995).

To further control for attention and eye movement as well as the many confounds associated with viewing of a stable 3-D perception elicited by the 2-D figure (e.g., visual processing associated with the presence of a stimulus on the screen; arousal secondary to task performance), several post-hoc analyses were conducted (p

We also report results of separate simple regressions that correlated measures of task difficulty and attentional control to activations associated with the selection of BFs. Quantifying task difficulty (i.e., the ability to volitionally select one visual interpretation per BF) ranked the Mach Pyramid as the most difficult and the Card as the easiest of the BFs. These task difficulty ratings were used in separate simple regression models to assess the possible mediating role of perceived difficulty in the recruitment of frontostriatal networks during the SELECTION relative to gaze FIXATION of BFs. We also correlated neuropsychological variables of attentional control derived from the CPT-II and the Stroop task to activation revealed during SELECTION minus FIXATION. Given the post nature of these analyses and our aim to assess only whether activation in frontostriatal regions would correlate with measures of behavior performance, the activation threshold was set at p -values

Results

Subject ratings indicate that of the five shapes, the Mach Pyramid was the most difficult (mean 3.1 ± 1.5) and the Card was the least difficult (mean 1.6 ± 0.5) to switch and maintain a percept upon the subject's first encounter with the stimuli. These two ratings differed significantly from one another (paired sample $t(8) = 3.04$, $p = .01$) (Table 1a). Other ratings did not differ significantly. FRONT and BACK orientations were comparable across figures.

Assessment of button press intervals for the perception of a stable percept during the scan session indicated that the mean MAINTENANCE duration for the FRONT orientation (35.70 ± 3.45) was similar to the BACK orientation (35.55 ± 3.90) across all figures (Table 1b). The mean time of SELECTION was also comparable for both the FRONT (3.30 ± 2.40) and BACK (3.18 ± 2.58) orientations across BFs. Participants were instructed to press the button if the figure faded in or out of a particular orientation once stable; however, these instances were too few for meaningful statistical analysis, most likely due to the proficiency participants obtained at BF orientation maintenance during the pre-scan training session.

Competing visual Perceptions-SELECTION relative to FIXATION

The analysis of the SELECTION condition relative to gaze FIXATION revealed bilateral activation of middle frontal gyri (BA8&9) encompassing dorsolateral prefrontal regions at the predetermined uncorrected p -value of .001, as well as when using a corrected p -value of .05. Other areas of activation revealed when using the predetermined threshold occurred within the left postcentral gyrus, left putamen, and left middle occipital gyrus (BA18). Right-sided activations occurred within the precentral, inferior temporal (BA37), and inferior occipital (BA18/19) gyri. Bilateral activation, albeit right greater than left, included superior frontal regions (BA9), the inferior parietal lobule (BA40), precuneus (BA19), and optic radiata (Figure 2).

Competing Visual Perceptions Revisited

To ensure adequate control of attention, eye movements, and stable 3-D viewing when attempting to determine areas of activation associated with the selection of BFs, separate post-hoc analyses compared the resulting contrast images derived from the SELECTION minus FIXATION to the MAINTENANCE period in the FRONT orientation and to the MAINTENANCE period in the BACK orientation.

Contrast analyses of SELECTION relative to FIXATION minus MAINTENANCE periods also revealed activation of frontostriatal regions during the selection of BFs. Thus, when activations during FRONT MAINTENANCE were subtracted from activations during the SELECTION relative to FIXATION, right superior and left middle (B A6) frontal regions as well as right anterior cingulate activations (BA24) were detected (Figure 2). Similar brain area activations resulted from the subtraction of activations during BACK MAINTENANCE from SELECTION relative to FIXATION activations (Figure 2).

Simple Regressions-Ratings of Task Difficulty

Mach Pyramid—Ratings on this BF (Figure ID; Table 1) positively correlated with the majority of activations seen in the SELECTION minus FIXATION contrast map (Figure 3A). Thus, areas of overlapping activation were detected in superior and middle (BA6&9) frontal regions bilaterally, encompassing dorsolateral prefrontal cortex and portions of the striatum, in addition to bilateral orbitofrontal gyri (B A32& 10), left anterior cingulate (B A32), and the thalamus, using our predetermined threshold p-level of .05 and a 4-voxel extent.

Card—Correlations of difficulty ratings with activations on this BF (Figure 1C; Table 1) overlapped minimally or not at all in frontostriatal regions with activations for SELECTION minus FIXATION (Figure 3B). Only a small region within the left superior frontal gyrus showed a positive correlation between Card ratings and activations for SELECTION minus FIXATION.

Simple Regressions - Neuropsychological Variables

IQ Scores—Higher IQ scores were associated with activation of superior prefrontal regions encompassing B A6 in the SELECTION minus FIXATION contrast (Table 2).

Only one regression involving CPT-II Commission Errors is reported as it pertains to frontostriatal involvement. No other regressions using the neuropsychological variables of the Stroop Interference score or the CPT-II d' T-score showed significant correlations with this region of interest previously documented during SELECTION minus FIXATION.

CPT-II Commission Errors

Commission errors ($M=7.00$; $s.d.=3.5$) correlated significantly with similar frontostriatal activations as those identified in the original SELECTION minus FIXATION contrast. Thus, greater activations in middle frontal regions encompassing B A8 accompanied fewer CPT-II commission errors. Significant correlations were also detected in the striatum (Figure 4).

Discussion

Consistent with previous accounts showing the involvement of frontostriatal pathways in top-down processing (Alexander, DeLong, & Strick, 1986; Tekin & Cummings, 2002), our results suggest that CSTC circuits help in selecting and maintaining a particular visuospatial interpretation of BFs: we found significant increases in fMRI signal in frontostriatal regions, including superior and middle frontal gyri, DLPFC, ACC, and basal ganglia (particularly the putamen) when participants select and maintain a specific perceptual interpretation of BFs. A

subtraction of FIXATION from SELECTION revealed significant fMRI signal in frontostriatal regions. Moreover, activations in these frontostriatal systems were present consistently during both SELECTION minus FRONT and SELECTION minus BACK contrasts. Our findings suggest that the frontostriatal system is likely involved in the active construction (i.e., selection) as well as the maintenance (i.e., neural upkeep) of a cued visual interpretation. In addition, frontostriatal activity correlated with IQ, suggesting a possible general relationship of activity in these constructional and maintenance functions with overall strength of cognitive abilities (Table 3). Additional correlations with indexes of selective attention and inhibitory control (i.e., Stroop and CPT-II, respectively) also suggest early alterations in the course of information processing. These correlations may represent manifestations of the role that top-down regulation can play in attentional control (Hillyard, Di Russo, & Martinez, 2004). Beyond showing that selecting a specific bistable-figure percept engages frontostriatal circuits, these collective findings pave the road to a more scientific understanding of the neural correlates of top-down control and self-regulation, two hallmarks of clinical hypnosis whereby certain individuals can change the way they experience themselves and the environment.

Neurophysiological studies in nonhuman primates have documented strong attentional influences over visual processing in multiple extrastriate cortical areas (Maunsell & Madams, 2000), findings that were replicated in the human primary visual cortex (Martinez et al., 1999) and even as early in the information processing stream as the lateral geniculate nucleus (Kastner, 2004). This modulatory process may account for the selection and maintenance of a specific visuospatial interpretation of BFs by employing attention in the context of cognitive control and self-regulation (Kosslyn, Thompson, Costantini-Ferrando, Alpert, & Spiegel, 2000; Posner, 2004b; Raz, 2004b; Rueda, Posner, & Rothbart, 2004). Whereas binocular rivalry involves perceptual alternations between competing monocular images (Tong & Engel, 2001), BFs lead to alternations between two possible pictorial interpretations. Previous studies have shown that observers can voluntarily control the alternation rate of both rivalry and BF reversal, suggesting that bistable perception may involve top-down control (Lumer, Friston, & Rees, 1998; Tong, Wong, Meng, & McKeef, 2002). In addition, attention can strongly influence dominance durations during BF reversal (Horlitz & O'Leary, 1993; Liebert & Burk, 1985; M. A. Peterson, 1986; Toppino, 2003). Finally, more recent findings examining the role of attentional selection on the modulation of dominance durations in bistable perception further support the notion that unlike binocular rivalry, which involves a more automatic, stimulus-driven form of visual competition, BFs are more easily biased by selective attention (Meng & Tong, 2004).

Whereas the study of attention has long been a central topic in experimental psychology, self-regulation and applications of clinical hypnosis have only recently become a central research concept within attentional control (Raz & Shapiro, 2002; Rueda, Posner, & Rothbart, 2004). Moreover, certain types of attention (e.g., resolving conflict, orienting, and alerting) can be construed as self-regulatory (Fan, Raz, & Posner, 2003; Raz, 2004a; Raz & Shapiro, 2002; Rothbart, Ellis, & Posner, 2004). Although many metaphors describe visual attention (e.g., attention as a spotlight or zoom lens), these similes exemplify the largely spatial conception assigned to attention in scientific experiments (Shalev & Algom, 2000). Investigators are still learning which specific visual operations attention can regulate (Raz & Buhle, 2006). We propose that in order to see BFs in a specific cued orientation, one might exercise a form of regulatory control over information processing in the visual streams during the time between presentation of the cue and the stimulus. Furthermore, many studies of the regulatory functions of attention have shown modulation of sensory systems (Posner, 2004b). These findings, pertaining to the regulation of sensory input by attention, suggest that modulatory mechanisms - hypnosis being one - are rather general and involve the processing of semantics, storing information in memory, generating emotions³, and selecting visual scenes (Posner & Rothbart, 1998; Rueda, Posner, & Rothbart, 2004).

Selection of visuospatial orientation can be induced in at least two general ways. One is a purely stimulus-driven fashion, as occurs with an abruptly occurring stimulus (Yantis & Jonides, 1990). The other, the focus of this study, is in a top-down fashion according to a preconceptualized cognitive schema, in response to voluntary commands or suggestions (GL Shuhnan, Astafiev, & Corbetta, 2004; G L. Shulman & Corbetta, 2004). Here, participants were trained to exercise effortful control⁴ in the selection and maintenance of one visuospatial orientation over another and to remain focused on it, because the perception of BFs typically oscillates spontaneously between two visuospatial orientations in the absence of such control (Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998). Upon presentation of the cue, even before the BFs are displayed, neural systems likely activate to engage the appropriate perceptual set (Driver, Eimer, Macaluso, & Van Velzen, 2004) and then to override or modulate incoming sensory activity (Kosslyn, Thompson, Costantini-Ferrando, Alpert, & Spiegel, 2000; Raz, Fan, & Posner, 2005; Raz, Moreno-Iniguez, Martin, & Zhu, 2006). This regulatory control may dampen the undesired alternative percept when the BFs appear (Rees, Russell, Frith, & Driver, 1999), or it may preferentially enhance activity of the desired alternative percept, thereby influencing which orientation of the object is perceived (Kosslyn, Thompson, Costantini-Ferrando, Alpert, & Spiegel, 2000; Raz, 2004b; Rees, Russell, Frith, & Driver, 1999).

Because the dominance periods during BF perception may have a stochastic component (Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972) and because voluntary and involuntary eye movements may influence how quickly percepts alternate (Einhauser, Martin, & Konig, 2004), pre-scan training exhorted participants to focus on the fixation point. This training continued until each participant demonstrated proficiency to select and maintain BFs' orientation without visible eye movements. Although we did not monitor eye movements in the scanner, the posttraining proficiency, as well as self-report of orientation stability - via a button press during the scan - suggest that eye movements did not influence our findings.

The selection and maintenance of a specific visual interpretation for BFs seems to involve frontostriatal components of CSTC circuits that link the cortex to the striatum, globus pallidus, and thalamus (Alexander, DeLong, & Stride, 1986; Tekin & Cummings, 2002). Cortical portions of CSTC circuits presumably contribute to self-regulation of behavior by modulating activity in the basal ganglia and thalamus, which in turn modulate activity in the cortex (Goldman-Rakic, 1996; Haber, Kowall, Vonsattel, Bird, & Richardson, 1986; Leung, Skudlarski, Gatenby, Peterson, & Gore, 2000; Parent & Hazrati, 1995; B. S. Peterson et al., 2002). Consonant with the feedback-loop characteristics of these circuits, the top-down effects that we report here accord well with the functions of CSTC circuits suggested by computational models that are based on the known anatomical connectivity of the component brain structures (Bar-Gad, Morris, & Bergman, 2003). Additionally, dysfunction of CSTC circuits has been postulated as the cause of a number of disorders of self-regulatory control, including Tourette syndrome, Obsessive-Compulsive Disorder, Attention-Deficit/Hyperactivity Disorder, and Bipolar Disorder (Blumberg et al., 2003; Casey et al., 1997; Graybiel & Canales, 2001; B. Peterson & Klein, 1997; Rosenberg, Dick, O'Hearn, & Sweeney, 1997; Rosenberg et al., 1997). At least some CSTC abnormalities manifest in impaired performance on such attentional tasks as the Stroop.

The Stroop task, which places demands on both self-regulatory and attentional capacities, activates a complex set of brain areas including the ACC, prefrontal cortices, and striatum (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Bush, Luu, & Posner, 2000; Kerns et al., 2004; B. S. Peterson et al., 2002; Raz et al., 2003a). Consistent with these findings, our results revealed that the Stroop interference measures correlated with prefrontal activations in the contrast of SELECTION minus FIXATION. Furthermore, consistent with the self-regulatory functions of frontostriatal circuits, fewer commission errors on the CPT-II accompanied

stronger frontostriatal activations on the BF task. Numerous reports point to the importance of prefrontal structures in representing and maintaining active task demands (Kane & Engle, 2002) and the role of the ACC in subserving the resolution and monitoring of conflict (Bush, Luu, & Posner, 2000; Carter, Botvinick, & Cohen, 1999; Kerns et al., 2004). However, the role of CSTC loops, and of frontostriatal connections in particular, has been relatively unexplored in health and disease (Blumberg et al., 2003; B. S. Peterson et al., 1998; Rinehart, Bradshaw, Brereton, & Tonge, 2002; A.L. Spessot & Peterson, 2004; A. L. Spessot, Plessen, & Peterson, 2004; van den Heuvel et al., 2003), as well as across development (Alexopoulos, 2002; Bradshaw & Sheppard, 2000; Orzhekhovskaya, 1990). Hypnosis, a selfregulatory process involving attention, is an excellent vehicle to elucidate these questions and apply them to specific pathologies.

Here we show that CSTC circuits, particularly their frontostriatal components, are likely involved in the effortful control of perceiving one orientation over another when viewing BFs. Interference from opposing percepts calls not only for attention to the preferred percept, but also for active inhibition of the undesirable one (Leopold & Logothetis, 1999). Consonant with prior studies delineating the anatomy and function of these circuits, our findings show that prefrontal areas typically associated with conflict resolution and monitoring, specifically the DLPFC and ACC acting in concert with subcortical nuclei, coordinate perceptual inhibition and selection as they regulate attention (Alexander, DeLong, & Stride, 1986; Chow & Cummings, 1999; Raz, 2004a; Saint-Cyr, 2003; Saint-Cyr, Bronstein, & Cummings, 2002).

Furthermore, our results demonstrate a significant relationship between neural activity in these systems and task difficulty. Frontostriatal activity increases when participants select and maintain the BFs that present the most challenging visuospatial orientation, as indicated by self-report (Figure 3 A). Conversely, when subjective task difficulty is minimal, our results with the priming cue (Figure 3B) are similar to findings of fMRI activations in prefrontal cortex during spontaneous perceptual shifts of BFs (i.e., shifts without the priming cue) reported previously (Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998). Because activity in frontostriatal pathways increases as participants select and maintain visuospatial orientations of BFs that are increasingly more difficult to stabilize perceptually, task difficulty may help explain how CSTC circuits influence the visual experience. One way in which frontostriatal activity may contribute to biasing the system towards a specific visual interpretation may be through inhibition of the undesired percept. Another may be through focus on priming the desired percept over the other. However, because recruitment of these frontostriatal pathways seems to occur as a function of task difficulty, inhibitory control seems the more likely explanation (Posner, 2004b).

While our findings address top-down influences in the visual domain, we speculate that such modulatory processes are likely to function in other sensory modalities and subjective experiences. The remaining papers in this Special Issue speak directly to this point. Circuits subserving the preferred perception of BFs may form a subset of self-regulatory circuits involving prefrontal cortex, ACC, and basal ganglia, and they may contribute to volitional control over wide-ranging psychological functions. Correlations of fMRI activity with general intelligence, for example, suggest that the ability to wield attentional control may involve a more general function of mental aptitude (Duncan, 2003; Duncan, Emslie, Williams, Johnson, & Freer, 1996). Toward this end, more recent behavioral and imaging studies have provocatively proposed that various forms of attentional training can enhance IQ (Klingberg et al., 2005; Klingberg, Forssberg, & Westerberg, 2002; Olesen, Westerberg, & Klingberg, 2004; Posner, 2004b). Thus, factors such as attentional effectiveness (Raz, 2004a) and measures of intelligence (Duncan, 2003) may advance the functional efficiency of the neural systems involved in the monitoring and resolution of conflict, and may even generalize to other control mechanisms. Hypnosis is a great lens to glean insights into self-regulation (Raz, Keller,

Norman, & Senechel, 2007), tease apart issues related to overt and covert control (Raz, Fan, & Posner, 2005), and elucidate the role of frontostriatal influence. We are currently conducting further studies to forward this work, using hypnotic suggestions where participants must change their visual representation within a repetition to elucidate the putative role of frontostriatal circuitry in involuntary as well as voluntary control. We hope to report on these results before long.

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