Item-specific Training Reduces Prefrontal Cortical Involvement in Perceptual Awareness

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Abstract

■ Previous studies on the neural correlates of perceptual awareness implicate sensory-specific regions and higher cortical regions such as the prefrontal cortex (PFC) in this process. The specific role of PFC regions is, however, unknown. PFC activity could be bottom–up driven, integrating signals from sensory regions. Alternatively, PFC regions could serve more active top–down processes that help to define the content of consciousness. To compare these alternative views of PFC function, we used functional magnetic resonance imaging and measured brain activity specifically related to conscious perception of items that varied in ease of identification (by being presented 0, 12, or 60 times previously). A bottom–up account predicts that PFC activity would be largely insensitive to stimulus difficulty, whereas a top–down account predicts reduced PFC activity as identification becomes easier. The results supported the latter prediction by showing reduced activity for previously presented compared to novel items in the PFC and several other regions. This was further confirmed by a functional connectivity analysis showing that the interaction between frontal and visual sensory regions declined as a function of ease of identification. Given the attribution of top–down processing to PFC regions in combination with the marked decline in PFC activity for easy items, these findings challenge the prevailing notion that the PFC is necessary for consciousness. ■

INTRODUCTION

Consciousness, the part of our mental life that we have a phenomenological experience of, has become a frequent topic of investigation in cognitive neuroscience. A consistent finding from studies of perceptual awareness is activity increases in regions related to sensory aspects of the stimulus used (Eriksson, Larsson, Åhlstrom, & Nyberg, 2007; Grill-Spector, Kushnir, Hendler, & Malach, 2000; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Sheinberg & Logothetis, 1997). In addition, a large body of evidence indicates that perceptual awareness is also correlated with activity in the prefrontal cortex (PFC) (Naghavi & Nyberg, 2005; Rees, Kreiman, & Koch, 2002). Although the role of sensory cortices in relation to conscious awareness may seem relatively straightforward (e.g., extracting information from sensory input), the prefrontal contribution remains unclear. Some theories propose a bottom–up driven role of the PFC. For example, Frith and Dolan (1996) suggested that posterior sensory regions define the content of consciousness and provide this content to frontal regions. This view is also consistent with theories that equate the content of consciousness with the content of working memory (Baddeley & Andrade, 2000; Courtney, Petit, Haxby, & Ungerleider, 1998). By contrast, other theories propose a top–down dominant role of the PFC in relation to conscious awareness (Crick & Koch, 2003; Dehaene &

Naccache, 2001). By this view, the PFC may work as a source of control that selects between possible competing interpretations. Alternatively, the PFC may contribute information that helps in the creation of an explicit representation. This may be accomplished by boosting existing representations (i.e., attentional amplification), or it may involve incorporating information generated in the PFC into relatively early perceptual processes (Bar et al., 2006). Viewed this way, it is possible that the need for top–down processes can be reduced in situations where little competition is present or with weak requirements on attentional resources (Tse, Martinez-Conde, Schlegel, & Macknik, 2005; Kosslyn et al., 1994).

Both neuroimaging research and single-cell recordings have shown that prefrontal activity can be modulated by manipulating ease of identification (Sigman et al., 2005; Bar et al., 2001; Rainer & Miller, 2000); that is, a less difficult identification process requires less prefrontal activity. However, it is unclear how this change is related to conscious awareness of the stimuli. We have previously developed a set of stimuli that can be used for studying neural correlates of consciousness (Eriksson et al., 2007; Eriksson, Larsson, Åhlström, & Nyberg, 2004). This is a set of pictures that are difficult to identify at first, hence, enabling a dissociation between stimulus parameters and conscious percepts (Figure 1A). However, by repeated exposure, they become significantly less difficult. In the present experiment, we trained participants to various extents on subsets of these pictures. We then

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Figure 1. (A) Example of the stimulus used, where an object is constituted by a subset of the lines in one color. This item is a duck in blue lines. (B) Untrained items took significantly longer to identify, whereas no difference was apparent between items previously seen 12 times (T12) compared to 60 times (T60). Mean identification time and standard deviation (error bars) in seconds for T12: 2.3, 0.8; for T60: 2.2, 0.9; and for untrained items: 8.8, 2.0.
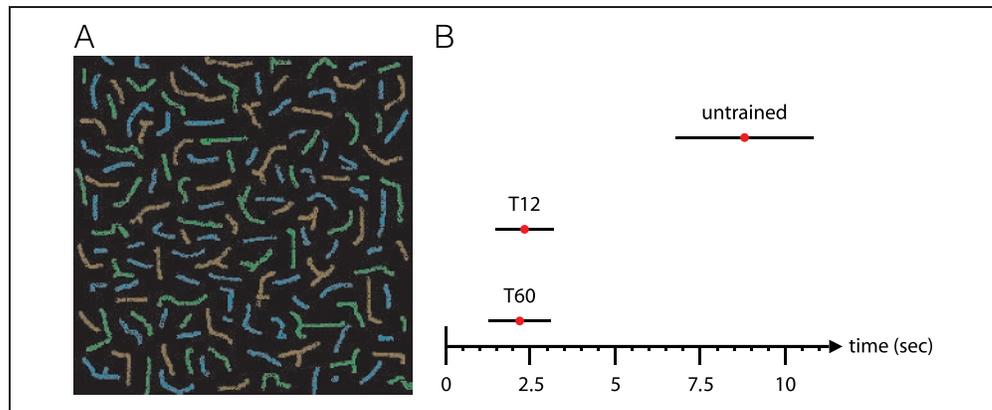
used high-field (3-T) functional magnetic resonance imaging (fMRI) to measure brain activity while participants identified trained and novel items. The results provide information on whether perceptual difficulty (i.e., high demands on attentional or other top–down regulatory mechanisms) is a factor influencing PFC activity related to consciousness, and thus, how one should view PFC involvement in conscious perception.

METHODS

Participants

Twelve normal subjects participated in this study (21–34 years of age, 6 women). All participants were right-handed by self-report, had normal or corrected-to-normal vision, and no one was color blind. Participants gave written informed consent, and the study was approved by the ethics committee at the University Hospital of Northern Sweden.

Stimulus Material, Training, and Experimental Phase

The stimuli consisted of 30 pictures of various animals and inanimate objects that had been modified to be difficult to identify (Figure 1A). Specifically, the lines making out the objects were fragmented and other lines were added to create a fairly homogenous array of short, "organic" lines. The object lines were in one of three colors (blue, green, or brownish orange) and the distractor lines were in all three colors (any given line had only one color).

In the training phase (the day before scanning), the participants viewed the pictures for an unlimited time on a PC running E-Prime 1.1 (Psychology Software Tools) and indicated successful identification by pressing a button on the keyboard. The picture then disappeared and the participant selected the name of the presented object from a list, thereby reporting what object had been identified. Five of the 30 pictures were presented 12 times (T12), and 5 were presented 60 times (T60), all in random order (with replacement). The remaining 20 pic-

tures were later presented as new items in the MRI scanner. Items constituting T12, T60, and new items were counterbalanced between participants, thereby controlling for any item-specific effects such as difficulty. Also, to minimize possible reliance on low-level features of the stimuli for identification, each item existed as three versions, with each version having a different color configuration. For example, a rabbit could be presented in blue, green, or brown/orange, with the color of the distractor lines changed accordingly. Each color configuration was presented equally many times.

In the scanner, the participants indicated identification by pressing a button. To allow a fuller "identification experience," the item presentation was left on for 1.0 sec after a response had been given. Each T12 and T60 item was presented four times (with different color configurations, repeating one configuration for the fourth presentation), making the three categories equal in size (20 items). All items were presented in random order with the restriction of having at least two items between repetitions of T12 or T60. If the participant did not identify the item within 50 sec, the trial was terminated. All trials were separated by an 8- to 10-sec presentation of a crosshair, constituting a low-level baseline.

MR Procedures

Data collection was made on a 3-T Phillips Achieva scanner (Philips Medical Systems, Netherlands). Functional T2*-weighted images were obtained with a single-shot, gradient-echo, echo-planar imaging sequence used for blood oxygenation level-dependent (BOLD) imaging. The sequence had the following parameters: echo time = 30 msec, repetition time = 2012 msec (43 slices acquired), flip angle = 90°, field of view = 22 × 22 cm, 64 × 64 matrix, and 3.4 mm slice thickness. The coil was an eight-channel SENSE head coil and a SENSE factor of 3.2 was used. To eliminate signals arising from progressive saturation, seven dummy scans were performed prior to the image acquisition. The stimuli and crosshair were projected on a semitransparent screen which the participants viewed through a tilted mirror attached to

the head coil. Presentation and reaction time data were handled by a PC running E-Prime 1.1 (Psychology Software Tools, USA) and Lumitouch fMRI optical response keypads (Photon Control, Canada) were used to collect responses.

Data Analyses

The data were analyzed in SPM2 (Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab 7.1 (Mathworks, MA, USA). All images were corrected for slice timing, realigned to the first image volume in the series, unwarped, normalized to the standard anatomical space defined by the MNI atlas (SPM2), and smoothed using an 8.0-mm full-width at half-maximum Gaussian filter kernel. Temporal autocorrelations were estimated using a first-order autoregressive model. Data were scaled over sessions and high-pass filtered with a cutoff of 128 sec. The model consisted of seven effects of interest (identification of T12, T60, new items, baseline, and the search periods preceding identification) and one effect of no interest. All regressors were convolved with a hemodynamic response function. Model estimations (restricted maximum likelihood) from each individual were taken into a second-level random effects analysis (t test) to account for interindividual variability. The statistical threshold was set to $p < .001$, uncorrected for multiple comparisons, $k \geq 5$.

ROI Analysis

Regions of interest (ROIs) were defined as spheres (10 mm radius) with the center coordinates taken from Table 2 in Eriksson et al. (2007). However, only the right inferotemporal (IT) coordinate was reported by Eriksson et al., although the cluster extended into both hemispheres. We therefore chose the subpeak within the left hemisphere part of the cluster that matched the right peak in respect of y and z coordinates. The same procedure was conducted for the right occipital ROI. Statistical threshold was set to $p < .05$, corrected for multiple comparisons within each ROI. Percent signal change data for Figure 3 were extracted with in-house software from a sphere (5 mm radius) centered in the coordinate averaged over all contrasts within the relevant ROI.

Connectivity Analysis

Psychophysiological interaction (Friston et al., 1997) aims at investigating how the interactions between two (or more) brain regions change as a function of an experimental parameter. This is, by large, equivalent to testing how regression slopes for the BOLD signal between the regions change across task conditions, in this case, identification of trained and untrained items. For each participant, we selected the coordinates for the peak voxel for either the untrained > T12 or untrained >

T60 contrast that was closest in space to the group dorsolateral prefrontal cortex (DLPFC) coordinate for untrained > T60 within the ROI ($x = 46, y = 14, z = 22$). For two participants, no voxel was significant for the training contrasts within the DLPFC, and we therefore used the group coordinate for these participants. We then extracted time-series data using the volume of interest tool in SPM2 (generating a representative univariate time series of a spherical region with 5 mm radius by using principal components analysis). Using the psychophysiological interaction tool in SPM2, we deconvolved the time series from a hemodynamic response function (HRF), multiplied each time point with the psychological variables of interest (-1 for T12 and T60, 1 for untrained items), and then reconvolved this new time series with the HRF (Gitelman, Penny, Ashburner, & Friston, 2003). This produced a time series representing the interaction between the manipulation (item-specific training) and the physiological response in the DLPFC. We then used this time series as an effect of interest in an ordinary SPM analysis. We also included the original BOLD time series and the psychological variables from the original analysis as covariates. Including these covariates has the effect of removing any variability explained by them, for example, the reduced level of BOLD signal as a result of training. We then looked at ROIs defined as spheres (10 mm radius) with center coordinates from Figure 3. Statistical threshold was set to $p < .05$, corrected for multiple comparisons within the relevant ROI.

Control Analyses

To make training of specific items efficient, we used a small number of items in the T12 and T60 categories (5 in each). Also, to get sufficient statistical power, we repeated each of these items four times in the scanner. Because repetition of stimuli has been shown to produce a reduction of activity in various brain regions (e.g., Henson, 2003), this could potentially confound the training effects as no untrained item was repeated. The possible suppressive effect on the BOLD signal due to repetition can be examined in a number of ways in the present design. First, we performed an analysis where the first two item repetitions were contrasted with the last two. Although ignoring the details of the repetition effects, this approach should capture its main effect because it makes relatively liberal assumptions about the data and has as many items per regressor as the training effects (20 items). The second statistical approach tried to account for the differences among repetitions by treating it as a parametric variable with four different levels. This amounts to including a parametric modulation of the T12 and T60 items in the model based on their order of appearance before estimating it. However, this model assumes linearity among levels (i.e., that the difference between the first and the second repetition is

the same as between the second and third, etc.), a condition that may not be fulfilled. As a third strategy, we therefore modeled each repetition as a separate regressor and looked at the conjunction between the different level contrasts (1st > 2nd ^ 2nd > 3rd ^ 3rd > 4th). This can be advantageous because the regressor for each level can be fitted independently of the others. However, the present experiment was not designed to detect repetition differences and the number of items for each level was low (5 T12 and 5 T60 items = 10 items for each level). For each analysis strategy, we then looked at the intersection between its contrast and the training effects (i.e., using the control contrasts as an inclusive mask), with a statistical threshold of $p < .001$, uncorrected, $k \geq 5$. That is, only regions with a spatial overlap between the control contrasts and the training contrasts are considered because a repetition effect must be present in the same regions as a training effect to be able to confound the results. To make sure that there was a difference between trained and untrained items that could not be due to stimulus repetitions, we also contrasted the untrained items with only the first presentation of the trained items (collapsing T12 and T60 items to get sufficient statistical power).

RESULTS

Behavioral Performance

Mean identification time in the scanner was significantly faster for the trained compared to the untrained items

$[F(1, 11) = 172.1, p < .001]$ (Figure 1B). There was no significant difference between T12 and T60 items $[F(1, 11) = 0.6, p = .46]$. These results show that training had a significant effect on performance, and that that no behavioral improvement was evident beyond 12 repetitions.

fMRI Results

Relative to a low-level baseline condition (viewing a fixation cross), identification of untrained items showed activation increases in large portions of the brain, including the occipito-temporal, parietal, lateral, and medial PFC (Figure 2A). This finding replicates previous research using the same stimulus material (Eriksson et al., 2004, 2007). The activation pattern was strongly reduced for T12 and T60 items. Importantly, the PFC contribution was markedly condensed compared to novel items. Overall, the extent of brain activity was reduced to about 23% as a result of training (number of significant voxels: untrained > baseline: 54,540; T60 > baseline: 12,790). If only counting voxels with $y > 10$ (i.e., approximately the PFC), brain activity extent was reduced to about 12% (untrained > baseline: 11,048; T60 > baseline: 904).

An important aspect of the present experimental design is its ability to isolate brain activity specific for the moment of identification, hence, conscious perception. Figure 2B (see also Figure 3) shows that pre-identification activity level is very similar between conditions and that the correlation between stimulus difficulty and PFC activity level is indeed specific for the moment of identifica-
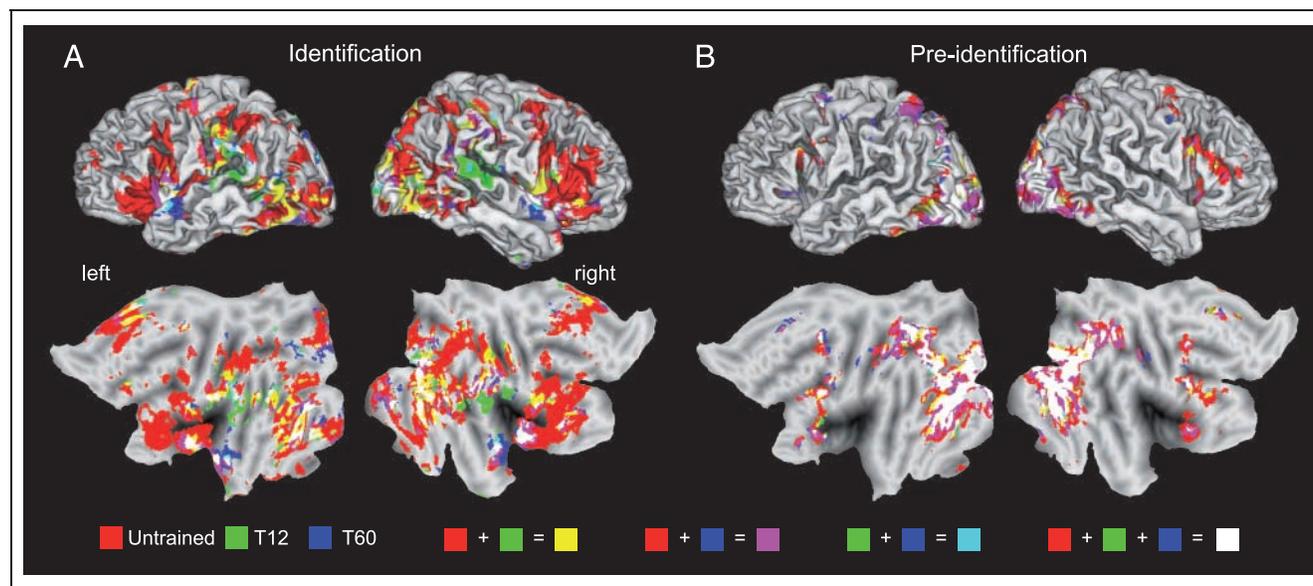
Figure 2. (A) Compared to a low-level baseline identification of untrained items (red) activated extensive regions in frontal, parietal, and occipito-temporal regions, thereby replicating previous research using the same stimulus material. Activation level was markedly reduced in the PFC and in several other regions for T12 (green) and T60 (blue) items. The lower part shows the activations projected on flat maps (Van Essen et al., 2001). (B) The effect of training was not apparent for the period preceding identification. Hence, the training effect was specifically associated with conscious awareness of object identity. To enhance spatial relations among conditions, z-value information has been removed. Hence, the colors signify a binary relation (i.e., "statistically significant") and are not modulated by the strength of the statistics. This enables a clearer interpretation of the color mixtures where conditions overlap (see Figure 3 for signal strength information).

Figure 3. Percent signal change for each ROI, showing that training on specific items lowers the need of cortical resources, most prominently in prefrontal and parietal regions, to achieve identification. Importantly, this was not the case for pre-identification activity. The first three bars in each subgraph represent signal change compared to baseline, and the last two represent the training-induced signal change (i.e., T12 and T60 compared to untrained items).

*$p < .05$ corrected for multiple comparisons; error bars = 1 standard deviation
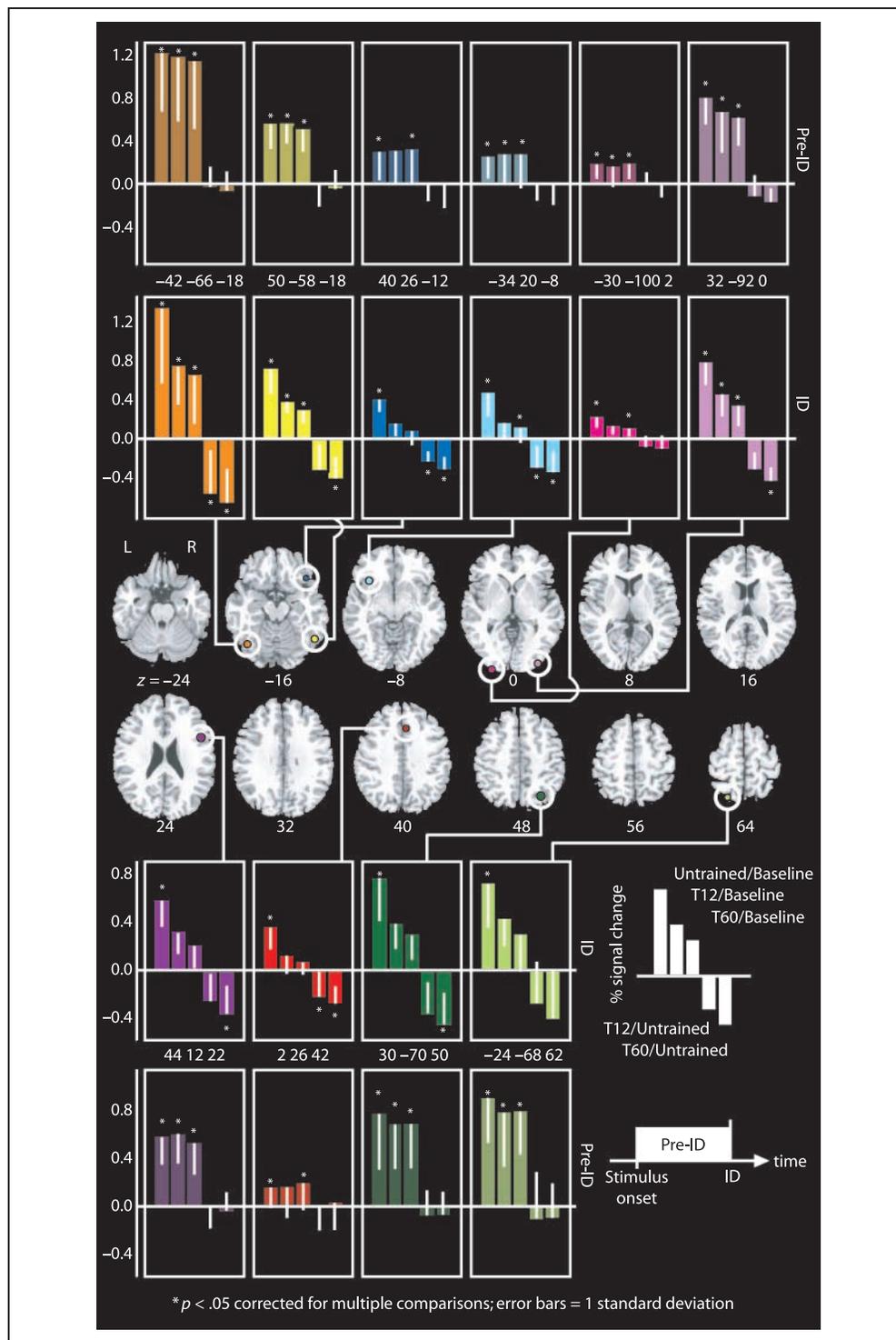
tion. A formal comparison between pre-untrained > pre-T12 and pre-untrained > pre-T60 revealed no consistent activation pattern (pre-untrained > pre-T12: cerebellum, -12 -64 -46, z-score = 3.93, -34 -58 -56, z-score = 3.56, right putamen, 32 -8 0, z-score = 3.39, ventral anterior temporal lobe, 46 -4 -42, z-score = 3.32; pre-untrained > pre-T60: left ventral orbito-frontal cortex, -30 28 -26, z-score = 3.81, brainstem, 4 2 -14, z-score = 3.80; pre-T12 > pre-T60: operculum, 52 -6 22, z-score = 3.59).

These results also show that activity level at identification does not reflect visual stimulation duration (e.g., by progressive saturation).

ROI Analysis

Based on previous results (Eriksson et al., 2007), we performed an ROI analysis on 10 regions that specifically have been related to conscious awareness: bilateral occipital

cortex, bilateral IT cortex, bilateral parietal cortex, bilateral ventral PFC, right DLPFC, and anterior cingulate cortex. Identification of untrained items, compared to baseline, led to increased activity in all ROIs (Figure 3). By contrast, only visual regions (occipital and IT cortices) were significantly activated by T12 or T60 items, with the exception of the left ventral PFC, which was also significant for T60 items.

To formally evaluate effects of stimulus difficulty, we directly compared T12, T60, and novel (untrained) items (Figure 3). Contrasting untrained > T12 confirmed that training caused a reduction of activity in all frontal ROIs except in the DLPFC. In posterior regions, only the left IT cortex was affected at this level of difficulty. Contrasting untrained > T60 showed a very similar pattern, although activation changes in the DLPFC and several posterior regions did now reach significance. The overall trend across examined regions was that T60 items were associated with a more pronounced activation decrease than T12 items, but no significant differences were seen in a direct contrast of T12 > T60. Thus, the activation data were in agreement with the nonsignificant difference in identification time for T60 and T12 items.

Connectivity Analysis

The reduction in frontal activity as a function of ease of identification indicates that fronto-posterior interactions were reduced for trained items. To formally test how the interaction between frontal and sensory regions was affected by the manipulation, we analyzed their functional connectivity (Friston et al., 1997). The DLPFC is one of the most consistently activated nonsensory regions in neuroimaging research on consciousness (Naghavi & Nyberg, 2005; Rees et al., 2002). Moreover, the PFC has been implicated as more generally involved in perceptual awareness than, for example, the parietal cortex (Eriksson et al., 2007). We therefore chose the DLPFC as the seed for the analysis (see Methods for details). A significant effect of training (collapsed across T12 and T60 items) was evident in the IT cortex and in the occipital cortex bilaterally (z-score right IT = 4.41, left IT = 3.67, right occipital = 3.82, left occipital = 3.69). These results confirm a change in functional connectivity between the PFC and sensory regions as a function of training (Figure 4). That is, for untrained items, sensory regions interacted more strongly with the PFC, whereas for trained items, sensory regions worked more independently of the PFC.

Control Analyses

None of the control analyses produced any significant result and it is therefore very unlikely that the training effects reported here were caused by stimulus repetitions during scanning. This lack of repetition effects is possibly due to the fact that the repeated items were
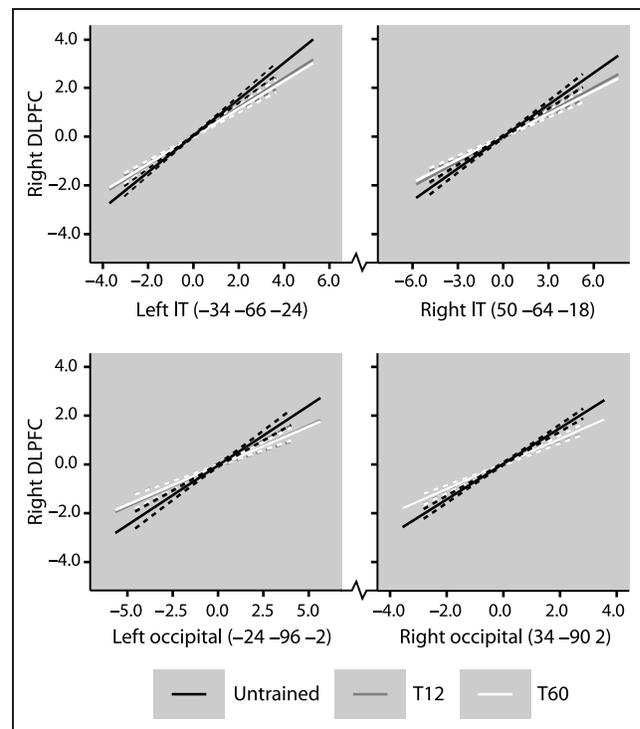
Figure 4. As a result of training on specific items, functional connectivity between the right DLPFC and visual sensory regions was reduced. This is illustrated by correlating BOLD signal (normalized, arbitrary units) in each region with that in the DLPFC for the first five scans, starting at the moment of identification for all trials for all subjects. A regression line was then fit for each condition (solid lines, dashed lines signify 95% confidence intervals). A 45° slope would indicate perfect correlation, hence, very strong functional connectivity between the two regions, whereas a flatter slope indicates less connectivity. The flatter slopes of T12 and T60, relative untrained, show that functional connectivity was reduced for trained items compared to untrained items.

trained, which may floor the response even for the first presentation. In addition, the use of different color configurations changed the physical appearance between repetitions. The contrast untrained > first presentation (T12 + T60) was significant in all ROIs except for the left parietal ROI ($p < .05$, corrected for multiple comparisons within each ROI), further confirming that the training effect was veridical.

DISCUSSION

The relation between PFC activity and consciousness has been very little explored, even though a large amount of data has implicated it as important. Here we used training on specific items to show that the interaction between the PFC and visual sensory regions changes as a function of ease of identification. Importantly, this was not the case for activity preceding identification, which was unaffected by the training. Although brain activity changes due to previous exposure have been extensively

documented previously (see e.g., Henson, 2003; Cabeza & Nyberg, 2000, for reviews), this is, to our knowledge, the first empirical investigation of training-induced changes specifically related to conscious awareness of object identity, dissociated from stimulus presentation.

The reduction of activity due to training is consistent with a top–down conception of PFC activity. If the PFC was a receiver of information, for example, as the maintenance component of working memory (Courtney et al., 1998) or as an information integration point (Baddeley, 2000), it is reasonable to assume that its activity level would be similar for trained and untrained items because a similar amount of information would be sent and/or integrated from sensory regions. By contrast, if the PFC is conceived of as an active participant in the creation of the content of consciousness, for example, by attentional control or by providing constraining information, activity level would be reduced for trained compared to novel items because a smaller amount of work would be needed due to the training. Admittedly, attention is generally thought of as an integrated part of the working memory architecture (Baddeley, 2003), and it has been hypothesized that working memory maintenance is at least partially achieved through attentional mechanisms (e.g., Awh, Vogel, & Oh, 2006). Thus, the description of working memory as representing a bottom–up prediction of the data may be seen as simplistic. However, for any sensory content to enter working memory maintenance, it needs to come *from* sensory regions, even if the process of selecting and/or maintaining that content is top–down.

Although the precise nature of the relevant top–down processes is unclear, previous neuroimaging research can be informative of possible interpretations of the present data. The ventral (v) PFC is a key region in a recent model by Bar et al. (2006) and is hypothesized to provide an "initial guess" of what is perceived and to incorporate this information to posterior perceptual processes. According to Bar (2003), vPFC activity level is modulated by how difficult the current percept is to resolve because a difficult percept is initially compatible with a larger number of identities, as the available information is less precise. A central part of the model is that the vPFC is using low spatial frequency information (shape) via the magnocellular pathway, which is faster than the parvocellular pathway in conveying high-frequency information (detail). The fragmented pictures used in the present experiment are practically devoid of low-frequency information, and so this information is not available. Instead, the vPFC may use whatever information is present, for instance, task instructions (Bar, 2003), which is identical between conditions. This is in line with the present results of equal level of activity between conditions before identification is made. The condition-specific activation levels at the moment of identification may then reflect a more extensive (short-term) information build-up through prefrontal–sensory

cortex interactions for difficult compared to easy items. That is, due to previous exposure, trained items may not need the same amount of PFC–sensory cortex interactions to achieve identification. This notion of vPFC activity is also consistent with conceptual priming, where priming effects are supposed to be a result of repeated semantic processing of a stimulus rather than of its physical attributes (see Schacter & Buckner, 1998, for a review). The present results can thus be interpreted as more efficient semantic processing in the aid of identifying the target (see also Schacter, Wig, & Stevens, 2007).

Other PFC regions are showing a similar activation profile as the vPFC, with a striking correlation between activation level and stimulus difficulty (as indicated by time to identification). Although not explicitly measured, this also correlates with a subjective characteristic of identifying these objects: the Aha!-experience. It has been shown that activity in the right DLPFC correlates with the amount of mismatch (surprise) in associative learning (Turner et al., 2004; Fletcher et al., 2001). Learning is here defined as "... the detection of a mismatch between predictions and outcomes together with an adjustment of expectancy on the basis of this mismatch" (Fletcher et al., 2001, p. 1043). Arguably, identification of novel items ("Aha!") should involve more learning adjustments than identification of trained items ("been there, done that..."). This also fits well with the proposed role of the vPFC in providing predictions about stimulus identity, with which comparisons can be made. Furthermore, the adjustments made as a consequence of a mismatch can be seen as a component of task set processes, which are executive functions that select and modulate downstream processes relevant for the present task (Miller & Cohen, 2001). According to Dosenbach et al. (2006), three different signal types are related to task set: task initiation, task set maintenance, and error signals for adjusting top–down processes. The regions identified as most consistently related to error signals and top–down adjustments by Dosenbach and others were the dorsal anterior cingulate cortex and the bilateral vPFC, matching the present results (see Figure 3). This is also in line with research on "Aha"-related brain activity during problem solving (Jung-Beeman et al., 2004; Mai, Luo, Wu, & Luo, 2004).

Regions other than the PFC also showed a training-related activity decrease. The parietal cortex has been discussed as being involved in conscious perception in a similar manner as the PFC (Rees et al., 2002). It is therefore noteworthy that we found a corresponding activity decrease in the parietal cortex. We also found that activity in IT regions, as in the PFC and the parietal cortex, was less for trained than untrained items. Previous research on perceptual learning has shown that visual cortex activity increases as an effect of training for stimuli that are difficult to perceive (Rainer, Lee, & Logothetis, 2004; Grill-Spector et al., 2000; Dolan et al., 1997), but

decreases for easily recognizable stimuli (Chao, Weisberg, & Martin, 2002; van Turennout, Ellmore, & Martin, 2000; Schiltz et al., 1999). This was further supported by a recent study by Kourtzi, Betts, Sarkheil, and Welchman (2005), showing that learning of low-saliency shapes increased activity in the lateral occipital complex, whereas learning of high-saliency shapes decreased activity in the same region. However, the stimuli used in the present experiment are not easily recognizable and the source of this discrepancy is not known. One possible interpretation of the present data pattern is that the PFC and the parietal cortex subserve executive processes that operate on visual regions such as the IT cortex. This interpretation is supported by the observation of reduced functional connectivity between the PFC and visual sensory regions as a function of item-specific training. Previous research has shown that attention can increase activity in sensory regions (Kanwisher & Vojciulik, 2000). It is therefore conceivable that once the top–down influences are lessened through training, IT cortex activity is reduced accordingly (e.g., attentional amplification is removed or reduced). Interestingly, this is also compatible with a predictive coding account. By this view, top–down signals represent a predictive code, much like Bar's ''initial guess'' (see above). When this top–down prediction meets bottom–up signals, they cancel each other out if the prediction is correct (Rao & Ballard, 1999). That is, a better fit between top–down and bottom–up signals results in a lower activity level at the point of convergence. The residual activity constitutes feed-forward error signals that adjust future predictions. This fits well with the present results of reduced IT cortex activity for trained compared to untrained items.

Previous research has indicated that priming-related reductions of BOLD signal may be due to a shift in peak latency rather than peak amplitude (James, Humphrey, Gati, Menon, & Goodale, 2000). However, inspection of the activity time courses showed that this was not the case for the present results, where a large amplitude difference stood out against few, very small, and inconsistently directed latency differences (data not shown).

Identification of target items in the fragmented pictures has only referred to explicit identification, although it is possible that implicit processing of target identity could have taken place before explicit identification was made. The possibility of implicit stimulus processing is well established (see Kouider & Dehaene, 2007, for a recent review), and research by Holm, Eriksson, and Andersson (in press) have shown that implicit identification of targets in the fragmented pictures can occur several seconds prior to explicit identification (see also Holm, 2007). This strengthens the interpretation of the present results as being specifically related to conscious awareness, rather than, for example, feature binding processes.

A potential role of the PFC in perceptual awareness that is compatible with the present results is that the PFC is not, by necessity, involved in creating a new conscious percept, but is engaged by certain experimental paradigms. If attention is viewed as a selective mechanism that enhances certain features while suppressing others, this may explain why attention has been deemed important for consciousness in paradigms such as inattentional blindness, change blindness, and the attentional blink (AB). That is, by selecting one thing over the other, the other may be actively pushed out of consciousness. This is in line with results from recent behavioral studies showing that performance can improve in the AB paradigm if attentional recourses are simultaneously occupied with other tasks (Olivers & Nieuwenhuis, 2005, 2006). This interpretation is further strengthened by electrophysiological measures demonstrating less attention-related brain activity for trials where the AB is weak (Slagter et al., 2007; Shapiro, Schmitz, Martens, Hommel, & Schnitzler, 2006). Also, a recent transcranial magnetic stimulation study showed that when presentation of the first target in the series (which, because attention is directed upon it, causes the second target to be missed) is accompanied with a magnetic pulse over the parietal cortex (which is assumed to interfere with the deployment of attention), the AB is ameliorated (Kihara et al., 2007). Hence, if attentional processes are decreased (by experimental manipulations, during trial to trial fluctuations, or by magnetic pulses), the ''unconsciousness'' induced by it is less severe. Thus, in tasks that rely on selection processes, conscious awareness of competing stimuli may be suppressed. However, in tasks where no competition is present, selection processes are not needed (see Koch & Tsuchiya, 2007 for a similar view). The inference from inattentional blindness, and so forth, may then not be that attention is necessary for consciousness, but rather, the less extreme statement that attention can influence what will enter awareness.

By this view, previous findings of PFC activity in relation to consciousness could, at least in part, have been caused by the use of stimuli that are difficult to perceive or interpret. Arguably, this applies to ambiguous/rivalrous stimuli (Srinivasan & Petrovic, 2006; Sterzer, Russ, Preibisch, & Kleinschmidt, 2002; Lumer & Rees, 1999; Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998), and to stimuli presented near threshold (Carmel, Lavie, & Rees, 2006; de Lafuente & Romo, 2005; Stephan et al., 2002; Dehaene et al., 2001; Sahraie et al., 1997) or in rapid succession (Kranzcioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Sergent, Baillet, & Dehaene, 2005; Feinstein, Stein, Castillo, & Paulus, 2004; Marois, Yi, & Chun, 2004; Kjaer, Nowak, Kjaer, Lou, & Lou, 2001). In other words, due to the use of difficult tasks, the bulk of previous research may have overestimated the role of PFC involvement for conscious perception. Admittedly, PFC activity is likely to be necessary for consciousness in certain situations, such as when the demands on attentional resources are high (Lavie, 2006; Mack & Rock, 1998). Still, the present results show that PFC involvement can be lessened and is

possibly even superfluous in other situations (Kouider, Dehaene, Jobert, & Le Bihan, 2007; Watkins, Shams, Tanaka, Haynes, & Rees, 2006; Tse et al., 2005; Bar et al., 2001). This would also apply to the proposed role of the PFC as providing guiding information for perceptual processes, as this is hypothesized to be important foremost under poor stimulus conditions (Bar, 2003). Indeed, with the exception of the left vPFC, only sensory regions reached a significant level of activity for trained items. This is important to take into consideration when building models of consciousness, or when trying to decide on necessary and sufficient conditions for consciousness to occur.

The present results support a top–down view of PFC involvement in consciousness akin to, for example, Crick and Koch (2003) and Dehaene and Naccache (2001). However, they also suggest that top–down processing may not be a requirement for consciousness because significant activity for trained items was located mainly in sensory regions. On the other hand, the nonsignificant results in the PFC and the parietal cortex cannot be taken as conclusive evidence that the contributing activity from these regions is naught. That is, statistically nonsignificant results are no guarantee that there categorically is no effect. In fact, one would expect some residual activity in these regions given that even the trained items are nontrivial to identify due to their fragmented nature. This is likely the reason for the remaining left vPFC activity for T60 items. Future research may provide additional evidence of the nonnecessity of PFC activity for consciousness.

In conclusion, difficulty of the identification task has great impact on consciousness-correlated activity in the PFC and a number of other regions. This has implications for how to interpret a large number of previous research reports on the subject of conscious perception, and may help to further refine theories of how consciousness is implemented in the human brain.

Acknowledgments

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