

The Salient Self: The Left Intraparietal Sulcus Responds to Social as Well as Perceptual-Salience After Self-Association

Jie Sui^{1,2}, Minghui Liu³, Carmel Mevorach⁴ and Glyn W. Humphreys²

¹Department of Psychology and Center for Biomedical Imaging Research, Biomedical Engineering Department, School of Medicine, Tsinghua University, Beijing 100084, China, ²Department of Experimental Psychology, University of Oxford, Oxford OX1 3UD, UK, ³Department of Psychology, Northeast Normal University, Chuangchun 130024, China and ⁴School of Psychology, University of Birmingham, Birmingham B15 2TT, UK

Address correspondence to Jie Sui. Email: jie.sui@gmail.com

Glyn W. Humphreys contributed equally to this work in terms of experimental design and writing up the paper.

Perceptual learning is associated with experience-based changes in stimulus salience. Here, we use a novel procedure to show that learning a new association between a self-label and a neutral stimulus produces fast alterations in social salience measured by interference when targets associated with other people have to be selected in the presence of self-associated distractors. Participants associated neutral shapes with either themselves or a friend, over a short run of training trials. Subsequently, the shapes had to be identified in hierarchical (global–local) forms. The data show that giving a shape greater personal significance by associating it with the self had effects on visual selection equivalent to altering perceptual salience. Similar to previously observed effects linked to when perceptually salient distractors are ignored, effects of a self-associated distractor also increased activation in the left intraparietal cortex sulcus. The results show that self-associations to sensory stimuli rapidly modulate neural responses in a manner similar to changes in perceptual saliency. The self-association procedure provides a new way to understand how personal significance affects behavior.

Keywords: fMRI, hierarchical stimuli, perceptual salience, self-association, ultrafast learning

Introduction

Human perception is subject to incremental learning through repeated exposure, which gradually changes the perceptual salience of behaviorally relevant stimuli. Changes in salience through experience-based perceptual learning have standardly been reported after several hours of practice (e.g., Karni and Sagi 1993; Watanabe et al. 2001; Li et al. 2009). What happens, however, if we make a social rather than a perceptual association to a stimulus—as when we associate a stimulus to ourselves rather than to other people? Do such self associations mimic changes in perceptual salience, and are effects of self and perceptual salience modulated by common brain mechanisms?

We have recently shown that there can be rapid behavioral changes in the response to neutral stimuli which are associated with ourselves rather than another person (Sui, He et al. 2012). We had participants learn an association between a geometric shape and label referring either to themselves, their best friend or a stranger. Subsequently participants were presented with the shape and a label and had to verify that the stimuli were paired correctly (the original shape-label pairings) or whether they were re-paired (e.g., the prior “self” shape was presented with the label for the best friend). Response times and accuracy were benefitted for matching shape-label pairs for the self compared with the best friend and stranger. The self-bias ro-

bustly occurred in different contexts and with contrasting task demands. In addition, self matching pairs showed weaker effects of contrast reduction compared with the other pairings, suggesting that there was enhanced perceptual processing for self-associated stimuli. Similar effects were found with stimuli associated with high relative to low reward, suggesting that the self-association effect might reflect differential reward values linked to the self compared with other people (Sui, He et al. 2012). We have also recently shown that this self-advantage in behavior is supported by a neural circuit involving the ventral medial prefrontal cortex (vmPFC) and the left posterior part of the superior temporal cortex (LpSTS). The coupling within this circuit increases for self-related stimuli compared with stimuli related to other people consistent with self-related representations in the vmPFC being linked to social attentional responses operating within the LpSTS (Sui et al. 2013). This evidence indicates that neutral stimuli (geometric shapes, in this instance) are able to rapidly acquire social salience by being associated with the self rather than with other people. We term this an effect of newly acquired personal significance. However, it is unknown whether the arbitrarily learned social salience of a stimulus can modulate visual selection, and, if it does, whether the effects are similar to the effects of perceptual salience on selection. This was examined here. Participants were asked to select target shapes in hierarchical forms, with the shapes either having high or low social salience by dint of their being associated with the self or with another person. Previous work on perceptual salience has focused on the functional and neural processes involved when we ignore perceptually salient distractors (Mevorach et al. 2006). We ask whether equivalent effects arise when social rather than perceptual saliency is manipulated, and salient self-related distractors have to be ignored.

Previous work on perceptual saliency has used a global/local task and hierarchical stimuli. In these experiments, global forms are made more salient by blurring the local elements, while using high contrast local elements differing in color increases the relative saliency of local forms (Mevorach et al. 2006, 2009, 2010). Responses to targets with low perceptual salience are disrupted by the presence of a distractor at the other level that has high perceptual salience, and the effect indicates that visual selection is modulated by the salience of stimuli and not simply by the level of the target within the hierarchical figure (though often there are also prioritized responses to targets occurring on the global relative to the local level, e.g., Navon, 1977). In particular, the selection of low salient targets correlated with increased activation in the

left intraparietal sulcus (IPS). Using TMS Mevorach et al. (2006) also showed that activity in the left IPS was associated with suppressing neural activity in the left occipital pole which would otherwise respond to high saliency distractors (Mevorach et al. 2010), since the application of TMS to suppress the left IPS led to increased activity in occipital cortex on trials with salient distractors. In the current study, we combined 1) self-association (Sui, He et al. 2012; Sui et al. 2013) to induce social salience and 2) a hierarchical visual recognition task to mimic the manipulations previously made to alter perceptual saliency (Mevorach et al. 2006, 2009, 2010). We asked whether functional and neural effects equivalent to those produced by perceptual changes can be introduced simply by making a self-related association to a stimulus—is there an effect of “socially salient” distractors, induced by self-association?

We conducted 4 experiments. First (Experiment 1), we carried out a baseline study to establish the relative dominance of local and global forms prior to the stimuli having self associations (in Experiment 3 and 4). Participants were presented with figures that comprised global squares, hexagon, or circles made up of local squares, hexagon, or circles, creating conditions in which the global shapes and their local elements were either congruent (e.g., local square comprising global square) or incongruent (e.g., local square comprising global hexagon). Different pairings of shapes were used in different blocks of trials. An effect of congruency when the task is to respond to either the global or local shape typically indicates the extent to which the nontarget level of shape competes for a response with the target level (Navon 1977; Mevorach et al. 2006), and we take this here as our operational definition of the relative saliency of the level of the stimuli (salient distractors are distractors that interference with responses to targets). Participants performed blocks of trials responding either to the global or to the local shapes. The target (global vs. local) and the congruency of the two levels of shape were varied. Next (Experiment 2), we manipulated perceptual salience to delineate how this affected performance. Perceptual salience was manipulated at both the local and global levels of the stimuli, to enable us to extract effects of perceptual salience across the different levels (see Mevorach et al. 2006). After this (Experiment 3), we had observers make social associations by initially associating the neutral shapes to labels for the self, a best friend and a stranger, giving observers just a short run of training trials. [Initially, a mean of 13.17 trials per association.] We asked whether self-associated stimuli affect performance in a manner that is similar way to effects with stimuli high in perceptual saliency (as in Experiment 2), demonstrating an effect of self-saliency. In Experiment 4, we used functional magnetic resonance imaging (fMRI) to evaluate the relations between the effects of self and perceptual saliency at a neural level.

If acquired self salience impacts visual selection in a similar manner to perceptual salience (Mevorach et al. 2006, 2009, 2010), we should find that visual selection is influenced the newly formed self-saliency of the stimuli, over and above effects of the level of the target (local or global). In addition, the selection of a low-salient target in the presence of a high-salient distractor should be associated with activity in the left IPS (Mevorach et al. 2009, 2010). The results verified this hypothesis. Both self and perceptual salience affected visual selection in a qualitatively similar manner; moreover, the rejection of a self-salient distractor was modulated through a region of the IPS previously shown to be recruited when perceptually

salient distractors are rejected (we use a region of interest (ROI) analysis based on Mevorach et al. 2009, and then replicate the result in a whole-brain analysis). The results suggest that associating sensory stimuli to the self produces rapid functional and neural changes equivalent to altering the perceptual saliency of stimuli. Our study provides a new way to understand how personal significance affects perception.

Experiment 1–3: Behavioral Studies

Materials and Methods: Experiments 1–3

Participants

In Experiment 1, 21 college students participated (4 males, aged between 19 and 29 years, $M = 23.52 \pm 2.23$). There were 24 college students (4 males, aged between 19 and 28 years, $M = 23.29 \pm 2.48$) in Experiment 2 and also in Experiment 3 (4 males, aged between 19 and 28 years, $M = 22.54 \pm 2.30$). All participants were right handed and had normal or corrected-to-normal vision. Informed consent was obtained prior to the experiment according to procedures approved by a local ethic committee.

Stimuli and Procedures

Different from prior work on perceptual salience where the stimuli were compound letters (Mevorach et al. 2006, 2009, 2010), shapes (circles, squares, hexagons) were presented in hierarchical (global–local) forms (in combinations of 2 shapes, across different trial blocks), and the task was to discriminate the shape at a global or local level in Experiment 1 (see Fig. 1a). Each local shape subtended $0.67^\circ \times 0.67^\circ$ of visual angle in width and height, respectively, and each global shape subtended $5^\circ \times 5^\circ$ of visual angle in width and height, respectively. In Experiments 1 and 3, the shapes were white solid figures, presented on a black background at one of two possible locations at above or below a white fixation of $0.58^\circ \times 0.58^\circ$ along the vertical midline. The center of each global shape fell 3.7° away from fixation. The experiment was run on a PC using E-prime software (Version 2.0) and the stimuli were displayed on a 21-inch monitor (1024×768 at 100 Hz).

Experiment 1 was a baseline study. The participants' viewing position was 80 cm away from monitor. Each trial started with a fixation cross in the center of the screen for 500 ms, followed by a compound, hierarchical stimulus above or below fixation for 150 ms and then the fixation cross returned during a response interval of 950 ms. Participants had to discriminate the shape at a global or local level by pressing 1 of 2 keys with the right index or middle finger. On half of the trials, the global and local shapes were the same (congruent trials); on the other half, the global and local shapes differed (incongruent trials). A white instruction (“global task” or “local task”) appeared at the center of the screen before each block, terminated by a key press from participants. The order of the tasks was counterbalanced within participants (ABBA or BAAB). Thus, there were two within-subjects variables—the target (global vs. local) and the congruency of the global and local shapes (congruent vs. incongruent). Each participant performed 4 blocks of 48 trials following 16 practice trials. Thus each condition consisted of 48 trials. The pairings of the shapes (circle and square, square and hexagon, hexagon and circle) were counter-balanced across participants using a balanced Latin square. In order to compare the results in Experiment 1 with those in Experiment 3, the design in Experiments 1 and 3 were identical except that the shapes in Experiment 3 had a social

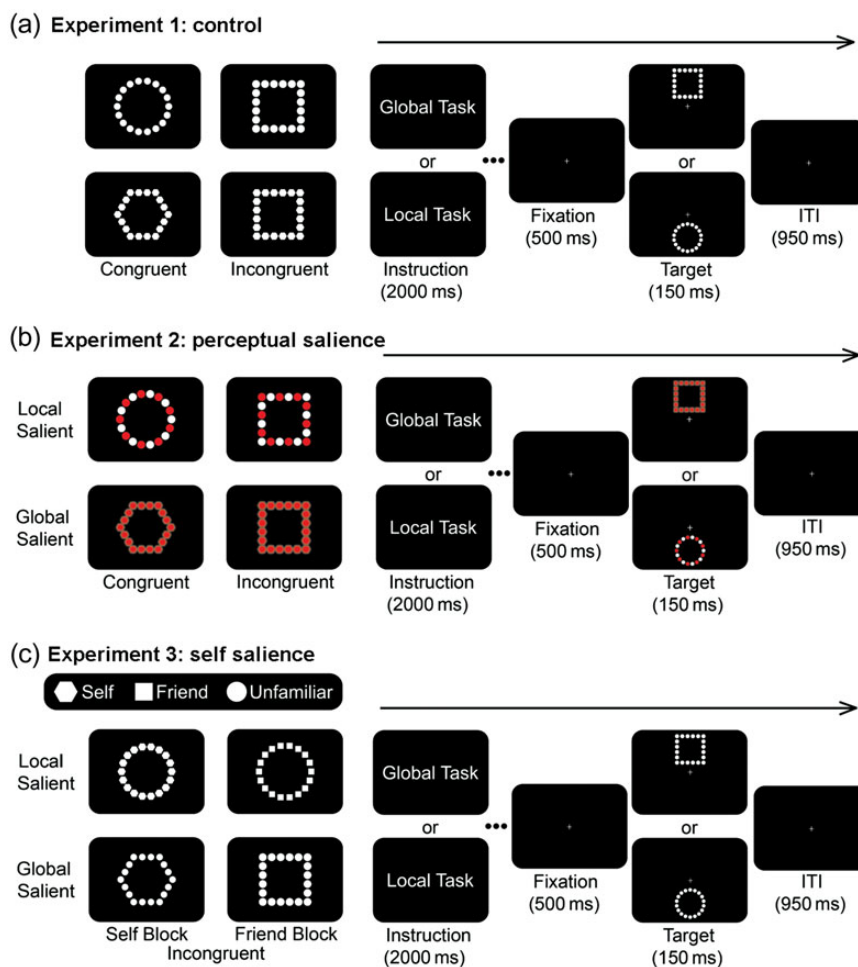


Figure 1. Examples of stimuli and procedures in Experiment 1 (a), Experiment 2 (b), and Experiment 3 (c). Three types of shapes (square, circle, and hexagon) in each experiment were counterbalanced across participants, and formed hierarchical shapes for the congruent and incongruent trials, and global-salient and local-salient trials. The targets appeared equally above or below fixation.

association. The stimuli and presentation conditions were identical in Experiments 1 and 3 where 1 shape (representing an unfamiliar other in Experiment 3) was paired with another 2 shapes (representing the self and a best friend in Experiment 3), in separate trial blocks to form the compound stimuli.

Experiment 2 used 2 types of compound stimulus: high local salience and high global salience (see Fig. 1b). Stimuli with high local salience had high contrast red and white local elements. Stimuli with high global salience had individually blurred red shapes (created using Adobe Illustrator CS4 with Gaussian Blur, with a radius of 7 pixels) (Mevorach et al. 2006, 2009, 2010). For congruent trials, when target and distractor levels vary in saliency, it is impossible to judge whether participants are responding to the appropriate level of the stimulus when the target has low saliency and the distractor high saliency (see Supplementary Table 1). In contrast, there is no ambiguity for incongruent trials, when the target has a different identity to the distractor(s). The analyses for Experiment 2 were performed on incongruent trials only. There were 2 within-subjects variables—target/distractor saliency (distractor salient vs. target salient) and the target (global vs. local). Each participant performed 8 blocks of 48 trials following 32 practice trials (48 trials per condition), with shape pairings counter-balanced across participants.

In Experiment 3, there were 2 phases. The responses to local-global forms were preceded by a simple shape-label association task. In the association task, participants were instructed to associate geometric shapes (e.g., a square, hexagon, and circle) with the self, their best friend and an unfamiliar other (counterbalancing the shapes across participants; see Sui, He et al. 2012). Participants had to orally repeat the associations between the shapes and each person, giving the name of their best friend or a name not associated with a person they knew, during the instructor phase of the experiment. After this, participants judged which of 3 labels matched a given shape. One shape and 3 labels (“You”, “Friend,” and “Stranger”) were presented respectively above and below a central fixation cross. Participants had to press 1 of 3 keys according to which label matched the shape. The distance between the central fixation cross and the center of the shape/the center of the 3 labels was 3°. A shape subtended $3.14^\circ \times 3.14^\circ$ of visual angle and the width and height of the 3 labels was, respectively, $9.0^\circ \times 1.0^\circ$. Each trial started with the presentation of a central white fixation cross for 2000 ms and then the shape-label display for 1000 ms during which participants had to make a response. Feedback was given. The task was terminated after 6 consecutive correct judgments were made. After a block of learning trials, participants completed the global-local task. In this task, there were blocks

of trials in which the self-associated shape was paired with the shape associated to an unfamiliar other (self vs. other discrimination) and blocks in which the friend-associated shape was paired with the shape associated to an unfamiliar other (friend vs. other discrimination). The task was to discriminate the shape-associated person (e.g., self vs. unfamiliar other, friend vs. unfamiliar other) at a given level of shape (global or local) (Fig. 1c). The order of the blocks (with self vs. other and friend vs. other discriminations, with the target at the local or global level) was counterbalanced within participants. Each participant performed 12 blocks (3 sets of 4 blocks—self vs. other, friend vs. other \times local or global target) of 64 trials following 32 practice trials (48 trials per condition). To reinforce the social coding of the stimuli throughout the subsequent trials with hierarchical shapes, the learning task was conducted 3 times, once before each set of 4 global–local blocks. The analysis on associative learning showed that participants were able to rapidly assign personal significance to neutral shapes, in line with prior studies (Sui, He et al. 2012; Sui et al. 2013) (see Supplementary Materials and Supplementary Fig. 1). For the global/local task, only the data for incongruent trials were analyzed. With congruent trials, any difference between the self/friend and the unfamiliar other conditions could reflect facilitated responding to the target level or disruption from the distractor level (as when perceptual saliency was manipulated in Experiment 2) (see Supplementary Table 2). The effects of the target and distractor levels could more clearly be separated on incongruent trials (when targets and distractors differed). There were 3 within-subjects variables—the task (self vs. unfamiliar other or friend vs. unfamiliar other), the saliency (distractor salient vs. target salient), and the target level (global vs. local).

To verify the effect of learned self saliency on selection, we also conducted 2 associative control experiments. One control experiment was identical to Experiment 3 except that we had participants judge the shape rather than the person tagged to the shape in the global/local task. In this case, implicit effects of the personal association were examined as the task did not require explicit responses to the associated information. The implicit experiment replicated the results in Experiment 3. To ensure that the result on self saliency was not simply due to

responses to the self-associated shape being faster than to shapes associated to other people, we conducted a further control experiment where, after personal associations were formed, participants carried out a person identification task where the association to a single shape (presented in the center of the screen so that selection of the target in a hierarchical shape was not stressed) had to be discriminated. In this case, the response was the same as in the hierarchical shape task (identify whether the self or other-associated shape was present at a given level in Experiment 3) but target selection was not required. There was no effect of self versus other discrimination with single shapes. This result rules out effects on response assignment while confirming effects of stimulus selection (when targets are selected from hierarchical figures) (see the Supplementary Materials).

Results and Discussion

Experiment 1: Baseline with Neutral Stimuli

There was no evidence of a speed-accuracy trade-off. To simplify the presentation RT and accuracy measures were combined in a single measure of response efficiency (RT/proportion correct, Townsend and Ashby 1983). A repeated measures ANOVA revealed significant main effects of target level, $F_{1,20} = 40.30$, $P < 0.001$, $\eta^2 = 0.67$, and congruency, $F_{1,20} = 10.09$, $P = 0.005$, $\eta^2 = 0.34$. There was no interaction, $P = 0.47$ (Fig. 2a). These results demonstrate both an overall global advantage (target level effect) and a congruency effect (worse performance with incongruent relative to congruent stimuli; Navon 1977; Fink et al. 1997; Hubner 2000; Yovel et al. 2001; Lux et al. 2004). There was no asymmetry in the congruency effect for local and global targets, indicating no differential access to stimulus information at the global and local shapes.

Experiment 2: Perceptual Saliency

A repeated-measures ANOVA on the efficiency data on incongruent trials showed significant main effects of target-distractor saliency [The analyses for Experiment 2–4 were performed on incongruent trials only. When target and distractor levels vary in saliency, it is impossible to judge whether participants are

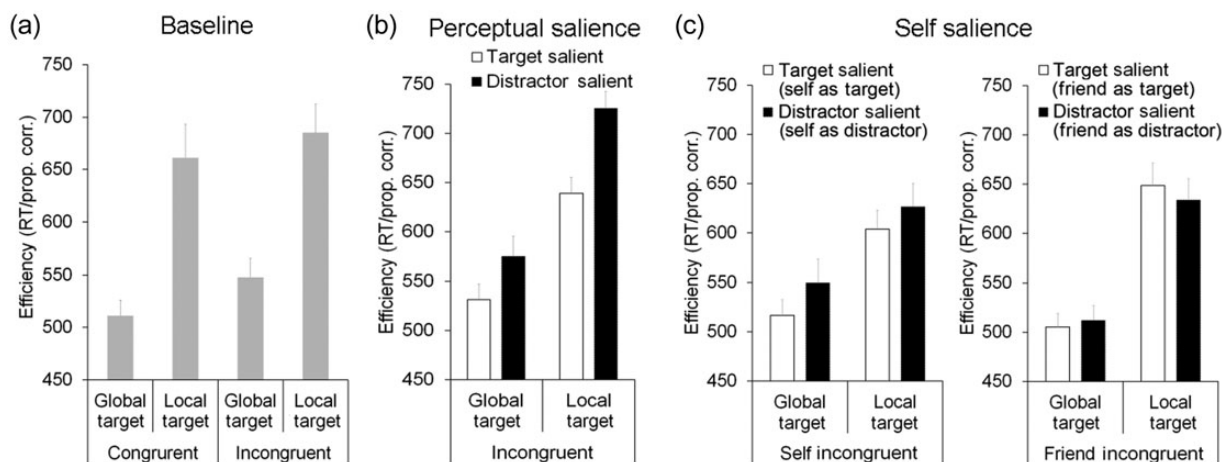


Figure 2. (a) The efficiency of responding as a function of the target (global vs. local) and item congruency (congruent vs. incongruent) in Experiment 1. (b) Experiment 2 manipulated the perceptual saliency of stimuli. The data show the efficiency for incongruent trials as a function of the level of target (global vs. local), and the saliency level (distractor-salient vs. target-salient). (c) Experiment 3 manipulated the self saliency of stimuli. The data demonstrated the efficiency of performance on incongruent trials as a function of the target (global vs. local), the task (self vs. unfamiliar other or friend vs. unfamiliar other), and the level of self saliency (distractor-salient vs. target-salient). Error bars represent standard errors.

responding to the appropriate level of the stimulus when the target has low saliency and the distractor high saliency. In contrast, there is no ambiguity for incongruent trials, when the target has a different identity to the distractor(s).], $F_{1,23} = 93.90$, $P < 0.0001$, $\eta^2 = 0.80$, indicating worse performance with high-salient distractors and low salient targets, compared with when targets had high saliency and distractors low saliency. There was also a significant effect of target, $F_{1,23} = 64.03$, $P < 0.001$, $\eta^2 = 0.74$, reflecting faster responses to global than to local targets. The interaction between target–distractor saliency and target level was also significant, $F_{1,23} = 8.09$, $P < 0.01$, $\eta^2 = 0.26$. Efficiency was reduced for both local and global targets when the distractor had high salience and the target low salience (compared with vice versa), $t_{(23)} = -8.09$ and -4.70 , P s < 0.001 for local and global targets, respectively (see Fig. 2b). The interaction arose because this saliency effect was stronger for local targets. The results were consistent with prior research where responses to hierarchical stimuli (rather than shapes, as used here, hierarchical letters in Mevorach et al. 2006, 2009, 2010, hierarchical gratings in Fink et al. 1999) were affected by perceptual saliency at both the local and global levels.

Experiment 3: Self-Saliency

We examined the interference effect on selection based on the self saliency of targets and distractors in the global/local task. A repeated-measures ANOVA on performance efficiency for incongruent trials was conducted with the factors being task (self/other vs. friend/other stimuli), self saliency (distractor salient vs. target salient), and level of target (global or local target). There was a significant 2-way interaction between the task and salience, $F_{1,23} = 5.53$, $P < 0.03$, $\eta^2 = 0.19$ (Fig. 2c). For the self vs. unfamiliar other task, there was a significant main effect of self saliency, $F_{1,23} = 8.05$, $P < 0.01$, $\eta^2 = 0.26$, indicating slowed responses when distractors had high saliency (i.e., distractors were associated with the self) and the target low saliency (linked to the unfamiliar other) compared with when distractors had low saliency (unfamiliar other) and the target high saliency (the self). There was no significant interaction between self salience and target level, $P = 0.46$, indicating that the interference effect occurred for both global and local targets. There was also a significant main effect of the target level, $F_{1,23} = 22.17$, $P < 0.001$, $\eta^2 = 0.49$; there were faster responses to global than to local targets. For the friend vs. unfamiliar other task, there was only a significant main effect of level of target, $F_{1,23} = 69.09$, $P < 0.001$, $\eta^2 = 0.75$. There was an overall benefit for global targets (as in Experiment 1) (Fig. 2c). Performance did not vary as a function of whether the shape associated with the friend was a distractor or target (P s > 0.26). The data indicate that the presence of the self shape uniquely affected selection across both local and global levels of the stimuli.

In sum, the behavioral data demonstrated interference from high saliency (self-associated) distractors on low saliency (unfamiliar other associated) targets, mimicking with the effects of perceptual saliency (in Experiment 2). Experiment 4 tested whether perceptual and self saliency operated through common neural structures (Mevorach et al. 2009, 2010).

Experiment 4: Neural Effects of Self Saliency

Materials and Methods

There were 12 right-handed participants (6 males, aged between 20 and 27 years, $M = 22.75 \pm 1.82$). The Method for Experiment 4

was identical to that in Experiment 3 except in the following aspects. Participants were first asked to associate one shape with themselves and another with their best friend. They then saw the self shape paired with a neutral shape for the global–local task. Each local element subtended $1.16^\circ \times 1.16^\circ$ of visual angle in width and height, respectively, and each global shape subtended $6.7^\circ \times 6.7^\circ$ of visual angle. The compound shape appeared on a black background at 1 of 2 possible locations above or below a white fixation cross of $0.5^\circ \times 0.5^\circ$, centered on the vertical midline. The task was to identify the shape on the target level rather than the person associated with the shape. Participants performed shape-label matching task before each of 3 fMRI runs. Each run consisted of 2 self blocks (global and local task); there were 96 experimental trials and 48 null trials in total. The order of the blocks was counterbalanced across runs.

fMRI Data Acquisition

We used a Siemens 3.0-T Trio MRI scanner to acquire T_2 -weighted echo planar images (EPI) blood oxygenated level-dependent (BOLD) contrast. Thirty-nine oblique slices were acquired with 2 mm thickness and 1 mm gap, with a plane resolution of 2.5×2.5 . We used, 90° flip angle, 33 ms echo time and 2300 ms slice repetition time. Images were acquired using an 8-channel phase array coil with a sense factor of 2. The slices covered most of the brain including the entire temporal cortex.

Data Analysis

The data were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm). EPI volumes were spatially realigned to correct for movement artifacts, transformed to Montreal Neurological Institute (MNI) standard space (Ashburner and Friston 2005), and smoothed using 8-mm Gaussian kernel to account for residual intersubject differences.

Statistical Analysis

A voxel-based analysis was performed in 2 steps. First, for each individual, we estimated the effect size on each condition averaged across the 3 sessions. We modeled the onset of each trial in each of experimental conditions (distractor/target salience \times target level). To correct for signal changes due to head movement, the 6 realignment parameters were also included. An additional set of harmonic regressors were used to account for any low-pass frequency variance within the data across time with a cutoff of 1/128 Hz, as well as the specific session effects. For each participant, we computed the averaged estimated response across the 3 sessions in each experimental condition. We focused on 4 experimental conditions on incongruent trials: distractor salient (self as distractor) in the global target condition, target salient (self as target) in the global target condition, distractor salient (self as distractor) in the local target condition, and target salient (self as target) in the local target condition.

ROI and Whole-Brain Analysis

In order to test the hypothesis that the self saliency of a stimulus impacts on visual selection in a similar manner to the effects of perceptual salience, we conducted a ROI analysis by extracting peak β values for each experimental condition from the left IPS region [$-30 -68 34$] implicated in rejecting salient distractors in prior work on perceptual salience (Mevorach et al. 2009). We also carried out a whole-brain analysis to verify

the ROI result. For the whole-brain analysis, we report those results showing a significant effect at $P < 0.005$ uncorrected across the whole brain and an extent threshold of >100 voxels.

Results and Discussion

Analysis of behavioral efficiency on incongruent trials revealed a reliable main effect of self-saliency (distractor salient vs. target salient), $F_{1,11} = 7.03$, $P < 0.03$, $\eta^2 = 0.39$. Performance was worse when the distractor had high social saliency (the self) and the target low social saliency (neutral), compared with when the distractor had low social saliency (neutral) and the target high social saliency (self). This is consistent with the data in Experiment 3. There was no significant main effect of the target level and no interaction between target and self saliency, $P = 0.35$ and 0.18 (Fig. 3*a*).

Similar to prior studies on perceptual saliency (Mevorach et al. 2009, 2010), we contrasted brain activation for incongruent trials for the self shape as a distractor to the self shape as a target. The ROI analysis, focusing on the left IPS [$-30 -68 34$] (see Mevorach et al. 2009) also revealed a significant main effect of self saliency, $F_{1,11} = 10.42$, $P < 0.01$, $\eta^2 = 0.49$; there was increased activation when the self was the distractor relative to when the self was the target (and the neutral shape was the distractor) (Fig. 3*b*). Neither the effect of the target level nor the interaction between target and self saliency were significant, $P = 0.76$ and 0.52 . In contrast, the similar analysis on the estimated β values extracted from the homologous region of the left IPS in the right hemisphere [$30 -68 34$] (Mevorach et al. 2009) did not reveal any significant effects of saliency ($P = 0.35$) or the target ($P = 0.18$), and there was no interaction ($P = 0.85$). Thus, increased activation in relation to the difficulty of rejecting the self salient distractor was confined to the left hemisphere. This result was confirmed by the whole-brain analysis. There was increased activation centered around the IPS (see Fig. 4*a*) when participants had to ignore the self (i.e.,

contrasting the self as distractor vs. the self as target). There was increased activity in the left IPS when the self was a distractor relative to when it was a target, for both local and global targets (Fig. 4*a*). We also explored the overlap for the whole-brain analysis for our study on self saliency (depicted in Fig. 4*a*) and the previous study on perceptual saliency (Mevorach et al. 2009) using the contrast (high-salient distractor $>$ high-salient target at both the global and local levels). This overlapping region [$-20 -64 44$] across the 2 studies is shown in Figure 4*b*. In order to demonstrate the common interference effect from self and perceptual saliency on selection in detail, the overlap of the self and perceptual saliency effects is plotted in the 3 coordinates—coronal, sagittal, and axial from the center of the overlapping region along 3 dimensions in Supplementary Figure 4. The results replicated the findings from studies of perceptual saliency and show a similar activity pattern (high-saliency distractors $>$ high-saliency targets) in common regions (Mevorach et al. 2009, 2010).

General Discussion

Experiments 1 and 2 here are baseline studies showing 1) local–global responses to neutral shapes (Experiment 1), and 2) effects of perceptual saliency when local and global levels are altered to selectively enhance their saliency (Experiment 2; see also Mevorach et al. 2006, 2009, 2010). Strikingly, these behavioral effects of perceptual saliency were replicated on neutral shapes briefly associated with the self relative to other people. Having the self-associated shape as a distractor rather than a target selectively disrupted performance while no such effect was found for shapes associated with a friend. This occurred for both global and local targets. Thus having the self-associated shape at the global level was equivalent to blurring the shapes, and having the self-associated shape at the local level was equivalent to making the local elements high contrast and different from each other. These effects arose after just a few (<15) learning trials, demonstrating that a new self-association rapidly transformed the saliency of the stimulus. While perceptual learning leads to exposure-based transformation of visual perception (Karni and Sagi 1993; Doshier and Lu 1998; Watanabe et al. 2001; Seitz and Watanabe 2003; Li et al. 2009), self-association with sensory stimuli generates a fast modulation effect equivalent to enhancing perceptual saliency.

We also measured brain activity to self-associated stimuli (Experiment 4) and showed increased activation when self salient distractors had to be rejected, with this increase selective to the same region as that found when participants reject perceptually salient distractors (taking an ROI from Mevorach et al. 2009). The results indicate that rapidly formed self-associations change the neural response in a manner that is qualitatively similar to effects produced by changing the perceptual saliency of stimuli. In particular, there was enhanced activation of left IPS when the task required participants to select the neutral shape and to ignore the self-associated shape. Previous studies have found activation of the left IPS when perceptually salient distractors have to be ignored (Mevorach et al. 2009, 2010; Melloni et al. 2012) and this has been causally linked with downregulation of early visual regions responding to the salient distractors (Mevorach et al. 2010; Melloni et al. 2012). For example, suppressive TMS applied to the left IPS leads to increased activity in early visual regions, consistent with the removal of top-down suppression from the

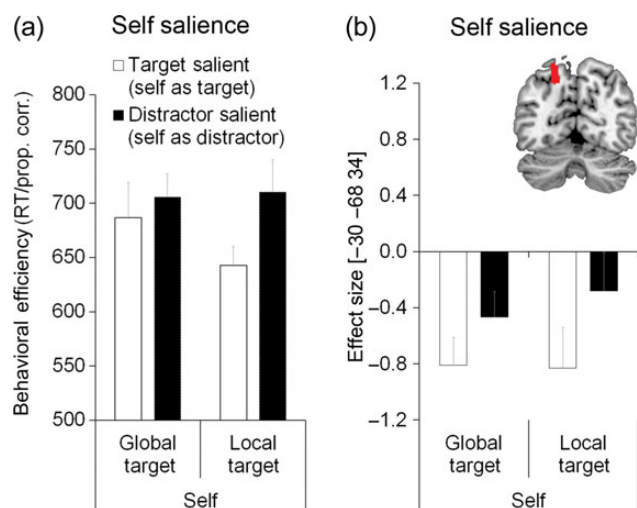


Figure 3. (a) Behavioral efficiency measures for incongruent trials as a function of the level of the target (global vs. local) and the level of self saliency (distractor salient vs. target salient) in Experiment 4. (b) ROI analysis on a region [$-30 -68 34$] from previous study of perceptual saliency (Mevorach et al. 2009). The peak estimate effect size on neural responses as a function of the level of saliency (distractor-salient vs. target-salient) and the level of the target (global vs. local). Neural responses were greater for the self shape as a distractor than for the self shape as target. Error bars represent standard errors.

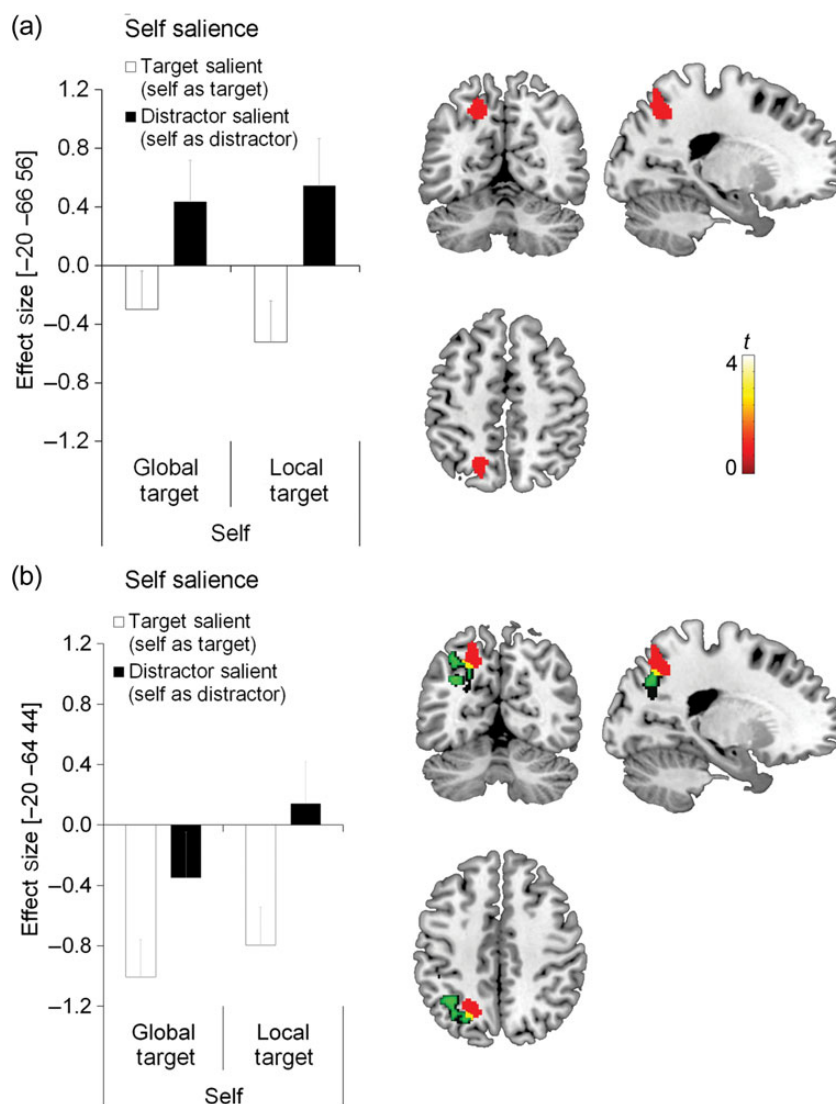


Figure 4. (a) The results of contrasting the self as a distractor vs. the self as a target in the whole-brain analysis in Experiment 4. The peak estimated β values for the effect of self salience were extracted from a region at $[-20, -66, 56]$ as a function of the level of salience (distractor-salient vs. target-salient) and the level of the target (global vs. local). Similar to the ROI result, neural responses were greater for the self shape as distractor than the self shape as target. Error bars represent standard errors. (b) Overlapping brain regions for the effects of self salience in Experiment 4 here and perceptual salience in Mevorach et al. (2009) using the comparison (salient distractor > salient target at both the global and local levels). Red represents brain regions showing an effect of self salience in Experiment 4; green represents the brain regions affected by perceptual salience in prior work; yellow represents the region of overlap across the 2 studies.

IPS. Here, we suggest that self-associated distractors engaged similar suppressive control processes when they had to be ignored. An alternative function of left IPS is associated with top-down control of spatial attention (Posner et al. 1984; Corbetta et al. 2000; Bressler et al. 2008; Bouvier 2009), but this effect typically occurs bilaterally, in both hemispheres. Some studies have also reported that the left parietal cortex is associated with local processing while right parietal cortex is related to global processing (e.g., Fink et al. 1997; Weissman and Woldorff 2005). These studies typically had participants to discriminate a target occurring at either the global or local level of a stimulus. In contrast, we had participants make a judgment to either global or local targets, and they did not need to shift spatial attention between global and local levels in a block. As shifts in spatial attention were not required, and since our effects occurred irrespective of the level of the target (global or local), our effects were unlikely to be due to shifts in spatial

attention or specialization of local versus global processes in the left IPS (e.g., Mevorach et al. 2009, 2010). The left IPS is also thought to be associated with motor control; in particular, the anterior part of left IPS is linked to hand movements and the posterior portion of the left IPS modulates visual feedback for movements (e.g., Thaler and Goodale 2011). In the current study, the effects are on visual selection not response control (see Supplementary Materials) and again seem unrelated to this alternative account of left IPS function.

The present evidence adds to other data in studies of the self showing that self-related information has high processing priority relative to other types of social information. For example, participants are faster to respond to their own than to other peoples' faces, both when the task requires explicit face recognition (categorizing faces as either the self or a familiar other) (Sui and Humphreys 2013), and when judgments about face orientation are required without explicit face recognition

(Keenan et al. 1999; Sui and Han 2007; Keyes and Brady 2010). Attention can also be automatically attracted by self-related information presented as a distractor compared with when distractors are associated with other people (Gronau et al. 2003; Brédart et al. 2006; Sui, Chechlacz et al. 2012). However, these studies have used highly familiar self-related stimuli learned over long periods of time, and they do not touch on whether new self-associations can quickly modulate stimulus selection. It is also difficult in such studies to rule out effects due to the perceptual properties of the particular stimuli. Here, we used neutral shapes and showed how self-associations modulate their selection in hierarchical forms (in the baseline study Experiment 1) to generate asymmetric interference from self-associated distractors (Experiment 3). Recent work has consistently shown the effect of personal association on perceptual matching in various contexts and with different task demands (Sui, He et al. 2012). In particular, personal associations engaged a core part of the self-representation network (vmPFC) and the social attentional network (LpSTS), and the strength of coupling between these 2 neural regions predicts the strength of personal association effects (Sui et al. 2013). The present study differs from these prior studies in focusing on whether the self saliency of a stimulus affects visual selection in a similar manner to the effects of perceptual saliency, and whether the neural response when self salient distractors have to be ignored matches that found when perceptually salient distractors are ignored (Mevorach et al. 2009, 2010). This change in focus generated substantial differences between the current study and our prior work (Sui, He et al. 2012; Sui et al. 2013). First, in prior work, participants always responded to the particular coupling of the associated shape and a label whereas here they respond directly to the associated identity of a shape, which was embedded within or formed a hierarchical figure (and required selection of the target shape from a distractor at the other level). Second, within the hierarchical shape, the self or familiar-other associated shape was always present along with a neutral (nonresponse-related) shape. Hence, we no longer see activation uniquely associated with the presence of the associated shape (e.g., in vmPFC and LpSTS), as it was also present in the contrast between the critical displays.

Following the current study, interesting questions remain about whether perceptual and self saliency interact in selection (i.e., when the 2 types of saliency co-vary). Prior work has showed that perceptual saliency operates in a bottom-up fashion, and responses to low-salient target in the presence of high-salient distractors leads to downregulation of distractor-driven activity in occipital visual cortex (Mevorach et al. 2010). In contrast self saliency may reflect top-down control processes when a set for the social association is formed. Whether this self association also modulates processing in early visual cortex is unknown. Some researchers have also argued that self-saliency may result from differential effects of reward (Behrens et al. 2008; Northoff and Hayes 2011) or positive emotion (Ma and Han 2010). For example, Sui, He et al. (2012) compared the effects of self-association with the effects of associating shapes to have different reward values. Perceptual matching was faster and more accurate for both self-associated shapes and shapes associated with high reward, and both forms of association led to reduced effects of stimulus contrast reduction on perceptual discrimination. These results suggest that self-saliency may reflect increased reward values linked to the self compared with other people. It is interesting too that

the association of high reward values to a stimulus has also been argued to change the perceptual saliency of the stimulus (e.g., Hickey and van Zoest 2012). Reward may be a common underlying mechanism linking self and perceptual saliency. This speculation should be tested in future research.

Overall, though, our evidence suggests that associating stimuli with the self can provide a new means of examining social modulation of perception without confounds from stimulus familiarity and complexity. Going beyond this, here we show that, once formed, personal associations can modulate the saliency of stimuli and subsequently impact on visual selection. We suggest that self-association can dynamically tune attention in the environment by altering the social saliency of stimuli.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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References

- Ashburner J, Friston KJ. 2005. Unified segmentation. *NeuroImage*. 26:839–851.
- Behrens TEJ, Hunt LT, Woolrich MW, Rushworth MFS. 2008. Associative learning of social value. *Nature*. 456:245–249.
- Bouvier SE. 2009. Top-down influences of spatial attention in visual cortex. *J Neurosci*. 29:1597–1598.
- Brédart S, Delchambre M, Laureys S. 2006. One's own face is hard to ignore. *Q J Exp Psychol*. 59:46–52.
- Bressler S, Tang W, Sylvester CM, Shulman G, Corbetta M. 2008. Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *J Neurosci*. 28:10056–10061.
- Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL. 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci*. 3:292–297.
- Doshier BA, Lu ZL. 1998. Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proc Natl Acad Sci USA*. 95:13988–13993.
- Fink GR, Marshall JC, Halligan PW, Dolan RJ. 1999. Hemispheric asymmetries in global/local processing are modulated by perceptual saliency. *Neuropsychologia*. 37:31–40.
- Fink GR, Marshall JC, Halligan PW, Frith CD, Frackowiak RSJ, Dolan RJ. 1997. Hemispheric specialization for global and local processing: the effect of stimulus category. *Proc Biol Sci*. 264:487–494.
- Gronau N, Cohen A, Ben-Shakhar G. 2003. Dissociations of personally significant and task-relevant distractors inside and outside the focus of attention: a combined behavioral and psychophysiological study. *J Exp Psychol Gen*. 132:512–529.
- Hickey C, van Zoest W. 2012. Reward creates oculomotor saliency. *Curr Biol*. 22:R219–R220.
- Hubner R. 2000. Attention shifting between global and local target levels: the persistence of level-repetition effects. *Vis Cogn*. 7:465–484.
- Karni A, Sagi D. 1993. The time-course of learning a visual skill. *Nature*. 365:250–252.

- Keenan JP, McCutcheon B, Sanders G, Freund S, Gallup GG, Pascual-Leone A. 1999. Left hand advantage in a self-face recognition task. *Neuropsychologia*. 37:1421–1425.
- Keyes H, Brady N. 2010. Self-face recognition is characterized by “bilateral gain” and by faster, more accurate performance which persists when faces are inverted. *Q J Exp Psychol*. 63: 840–847.
- Li S, Mayhew SD, Kourtzi Z. 2009. Learning shapes the representation of behavioral choice in the human brain. *Neuron*. 62:441–452.
- Lux S, Marshall JC, Ritzl A, Weiss PH, Pietrzyk U, Shah NJ, Zilles K, Fink GR. 2004. A functional magnetic resonance imaging study of local/global processing with stimulus presentation in the peripheral visual hemifields. *Neuroscience*. 124:113–120.
- Ma Y, Han S. 2010. Why we respond faster to the self than to others? An implicit positive association theory of self-advantage during implicit face recognition. *J Exp Psychol Hum Percept Perform*. 36:619–633.
- Melloni L, van Leeuwen S, Alink A, Müller NG. 2012. Interaction between bottom-up saliency and top-down control: how saliency maps are created in the human brain. *Cereb Cortex*. 22:2943–2952.
- Mevorach C, Hodsoll J, Allen H, Shalev L, Humphreys GW. 2010. Ignoring the elephant in the room: a neural circuit to downregulate salience. *J Neurosci*. 30:6072–6079.
- Mevorach C, Humphreys GW, Shalev L. 2006. Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nat Neurosci*. 9:740–742.
- Mevorach C, Shalev L, Allen HA, Humphreys GW. 2009. The left intraparietal sulcus modulates the selection of low salient stimuli. *J Cogn Neurosci*. 21:303–315.
- Navon D. 1977. Forest before trees - precedence of global features in visual-perception. *Cogn Psychol*. 9:353–383.
- Northoff G, Hayes DJ. 2011. Is our self nothing but reward? *Biol Psychiatry*. 69:1019–1025.
- Posner MI, Walker JA, Friedrich FJ, Rafal RD. 1984. Effects of parietal injury on covert orienting of attention. *J Neurosci*. 4:1864–1874.
- Seitz AR, Watanabe T. 2003. Is subliminal learning really passive? *Nature*. 422:36.
- Sui J, Chechlacz M, Humphreys GW. 2012. Dividing the self: distinct neural substrates of task-based and automatic self-prioritization after brain damage. *Cognition*. 122:150–162.
- Sui J, Han S. 2007. Self-construal priming modulates neural substrates of self-awareness. *Psychol Sci*. 18:861–866.
- Sui J, He X, Humphreys GW. 2012. Perceptual effects of social salience: evidence from self-prioritization effects on perceptual matching. *J Exp Psychol Hum*. 38:1105–1117.
- Sui J, Humphreys GW. 2013. The boundaries of self face perception: response time distributions, perceptual categories, and decision weighting. *Vis Cogn*. 21:415–445.
- Sui J, Rotshtein P, Humphreys GW. 2013. Coupling social attention to the self forms a network for personal significance. *Proc Natl Acad Sci USA*. 110:7607–7612.
- Thaler L, Goodale MA. 2011. Neural substrates of visual spatial coding and visual feedback control for hand movements in allocentric and target-directed tasks. *Front Hum Neurosci*. 5: doi: 10.3389/fnhum.2011.00092
- Townsend JT, Ashby FG. 1983. Stochastic modelling of elementary psychological processes. Cambridge (UK): Cambridge University Press.
- Watanabe T, Nanez JE, Sasaki Y. 2001. Perceptual learning without perception. *Nature*. 413:844–848.
- Weissman DH, Woldorff MG. 2005. Hemispheric asymmetries for different components of global/local attention occur in distinct temporo-parietal loci. *Cereb Cortex*. 15:870–876.
- Yovel G, Yovel I, Levy J. 2001. Hemispheric asymmetries for global and local visual perception: effects of stimulus and task factors. *J Exp Psychol Human*. 27:1369–1385.