

When the Brain Loses Its Self: Prefrontal Inactivation during Sensorimotor Processing

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Summary

A common theme in theories of subjective awareness poses a self-related “observer” function, or a homunculus, as a critical element without which awareness can not emerge. Here, we examined this question using fMRI. In our study, we compared brain activity patterns produced by a demanding sensory categorization paradigm to those engaged during self-reflective introspection, using similar sensory stimuli. Our results show a complete segregation between the two patterns of activity. Furthermore, regions that showed enhanced activity during introspection underwent a robust inhibition during the demanding perceptual task. The results support the notion that self-related processes are not necessarily engaged during sensory perception and can be actually suppressed.

Introduction

Life is an art, and like perfect art it should be self-forgetting.

—Suzuki, 1964

To what extent are self-representations engaged during sensory perception? Surprisingly, this fundamental question is far from being experimentally resolved. The notion that an “observer” function or a “homunculus” is a critical ingredient of sensory perception has been a common theme in a number of models of subjective perception. Given a more concrete neuroanatomical interpretation, these theories propose that subjective awareness involves a kind of interplay between sensory cortex and self-related prefrontal cortex. Thus, in a recent extension of the “global work space” metaphor of consciousness, Baars et al. (2003) suggest that conscious perception may entail a dialog between specific self-related prefrontal regions and sensory cortex. Similarly, Crick and Koch suggested a view of representations in the front of the brain having a “homunculus” function, “observing” the sensory back of the brain (Crick and Koch, 2003).

Quite paradoxically, during truly intense sensory perceptual states—such as watching an absorbing movie, or being involved in a highly demanding sensory task—the strong subjective feeling is of “losing the self,” i.e., of disengagement from self-related reflective processes. It can be argued, and indeed has been proposed (Crick and Koch, 2003), that the self-related homunculus function is an automatic, subconscious

process and consequently can not be directly accessible to the perceiving individual. With the advent of functional brain imaging, this question is now experimentally tractable, since it is now possible to observe brain activations that may be associated with subconscious processes as well (Hannula et al., 2005).

Reviewing the relevant literature of brain imaging, it is clear that a lot of data exist with regards to sensory cortex on the one hand, and self-related regions on the other—but very little information is available concerning their potential interplay or coactivation.

In the domain of sensory perception, the advance in our understanding has been truly dramatic, leading to quite a highly detailed understanding of the basic functional anatomy of human sensory cortex. Reviewing this data is of course beyond the scope of this introduction. Suffice it to say that we have a fairly consistent picture of the layout of the hierarchy of cortical areas leading from early V1 to high-order occipitotemporal object areas such as the lateral occipital complex (LOC; Malach et al., 2002), and major specializations such as face-selective cortex in the fusiform gyrus are all examples of robust and consistent activation patterns produced by sensory stimulation (for reviews, see Grill-Spector and Malach, 2004; Tootell et al., 1996). Similarly, in auditory cortex, sensory representations have been described at an increasingly fine detail (Formisano et al., 2003).

With regards to the other element of this study, that of self-related cortical areas, the situation is more complex. While the existence of a psychological structure of “self” has been a central and established concept in psychoanalytic literature (James, 1890; Wolf, 1988), its neuroanatomical correlates have only recently become a focus of detailed research. Nevertheless, recent neuroimaging work actually provides a surprisingly consistent set of converging activation patterns. A number of studies have addressed the issue of self-representations. These studies highlighted consistent cortical regions, such as medial prefrontal cortex (PFC), especially its dorsal part extending somewhat to dorsolateral PFC, the anterior and posterior part of the cingulate cortex, and more laterally the inferior parietal cortex (IPC) (Schmitz et al., 2004; Gusnard et al., 2001; Johnson et al., 2002; Keenan et al., 2000; Kelley et al., 2002).

Some of these studies point to a clear hemispheric specialization within the broad spectrum of self-related functions, with the right hemisphere engaged during self-image processing, such as watching self-face images compared to popular faces (Keenan et al., 2000; Schmitz et al., 2004), while the left hemisphere is engaged during internally cued responses (Gusnard et al., 2001). Interestingly, at least part of this network appears to be involved also in attributing mental state to others (Schmitz et al., 2004), which can be effective in allowing predictive power of behavioral responses—the so-called “theory of mind” (Vogeley et al., 2001; Gallagher and Frith, 2003). This potential link is intriguing, since it may offer a role for self-representations in social cognition (Frith and Frith, 1999; Stuss and Anderson, 2004). However, the issue of self-related activations, their

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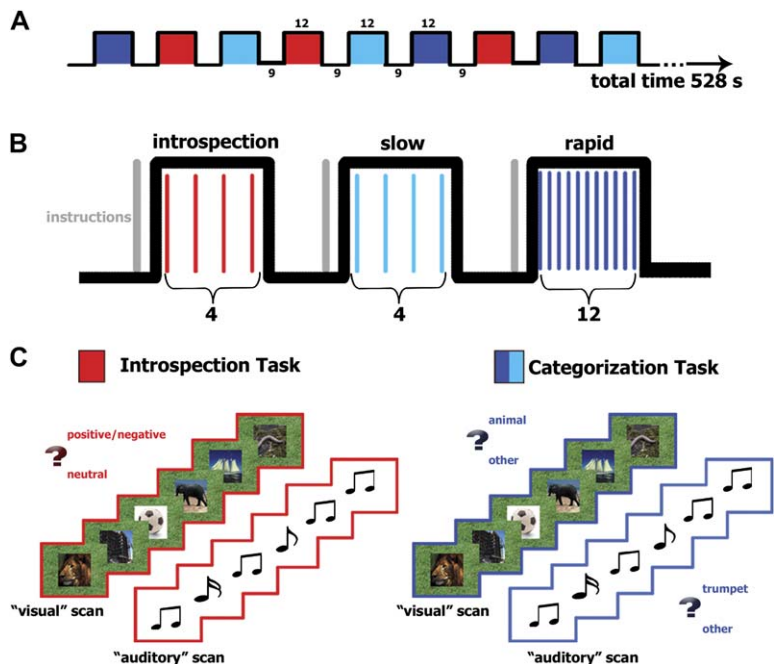


Figure 1. Experimental Design and Stimuli Used in the Visual and Auditory Scans

(A) Block design used in both visual and auditory scans. Red epochs represent the “introspection” condition, and dark and light blue represent the “rapid” and “slow” categorization conditions, respectively.

(B) Number of stimuli in each of the three experimental conditions (vertical colored bar): “rapid” categorization epochs contained 12 stimuli in each block, while “slow” categorization and introspection epochs contained four stimuli. Prior to each block, a visual cue instructed subjects what task to do (vertical gray bar).

(C) Stimuli used in experiment. Note that the same set of stimuli (pictures and audio clips) was used in both tasks. During the introspection task, subjects inspected the stimuli and self-introspected about the emotional responses elicited in them by the stimuli (high-arousal versus neutral). During the categorization task, subjects categorized stimuli into categories: animal versus others in the visual scan, trumpet versus other in the auditory scan.

overlap with other functions, and their hemispheric lateralization is still under debate (Morin, 2002; Turk et al., 2002, 2003). More generally, it is important to emphasize that the extent to which self-related processes involve a single, unified neural entity or rather a cluster of weakly associated functions remains to be elucidated.

These results have actually been anticipated by a detailed neuropsychological literature that has documented various aspects of self-image, personality characteristics, planning, and decision making to be disrupted by prefrontal damage (Damasio et al., 1994; Kolb, 1990; Luria, 1973; Turk et al., 2002).

To conclude, despite its seemingly ill-defined and multidimensional nature, converging neurological and psychological evidence indicates that self-related representations are associated with a consistent and reproducible set of brain structures.

Given this substantial body of neuroimaging data related to sensory perception on the one hand, and self-related processes on the other, it is surprising that very few studies have directly addressed the question of the interplay between the two—i.e., to what extent do self-related regions and sensory cortex coactivate during sensory perception?

In a recent study, Gusnard and colleagues (Gusnard et al., 2001) found an interesting preferential activation in dorsomedial PFC during introspection versus an external processing task, suggesting a specialization of this region for self-related emotional processing. However, introspection is a very high-level cognitive task that may include, in addition to the emotional self-related aspects, also increased attentional, memory, and cognitive demands, so it is not clear what the actual source of the preferential activation in this study was.

Here, we addressed this problem directly by manipulating both the self-awareness level and the processing load during our experiments. To map self-related representations, we chose self-introspection as the most rel-

evant self-engaging task (James, 1890) and compared it to activity patterns induced by sensorimotor categorization tasks. Critically, to disentangle the possible role of attentional effects, we studied this relationship under two different levels of processing loads. Our results show a clear segregation between regions engaged during self-related introspective processes and cortical regions involved in sensorimotor processing. Furthermore, self-related regions were inhibited during sensorimotor processing. Thus, the common idiom “losing yourself in the act” receives here a clear neurophysiological underpinnings.

Results

The aim of this fMRI study was to directly compare, during the same scan, self-related processes with highly engaging sensory processes, all the while trying to keep the sensory stimuli and motor responses as similar as possible. To that end, we employed the experimental design depicted in Figure 1. The experiment was conducted in both the visual and auditory domains and consisted of three conditions: (1) an easy categorization condition (“slow”), in which subjects categorized visual and auditory objects presented at a slow rate (one stimulus/3 s.); (2) an introspective condition (“introspection”), having identical stimuli and motor responses except that subjects were required to self-introspect about their own emotional responses (aroused versus neutral) toward these stimuli, as used in previous experiments (Bradley and Lang, 1994; Rotshtein et al., 2001); and (3) a difficult categorization task (“rapid”) similar to the “slow” condition but at triple the stimulation rate. Thus, “slow” and “introspection” conditions were identical in terms of sensory stimuli and motor output but differed in the cognitive task. On the other hand, “slow” and “rapid” conditions were similar in the cognitive task but differed in the sensorimotor processing and attentional loads. Behavioral measurements verified

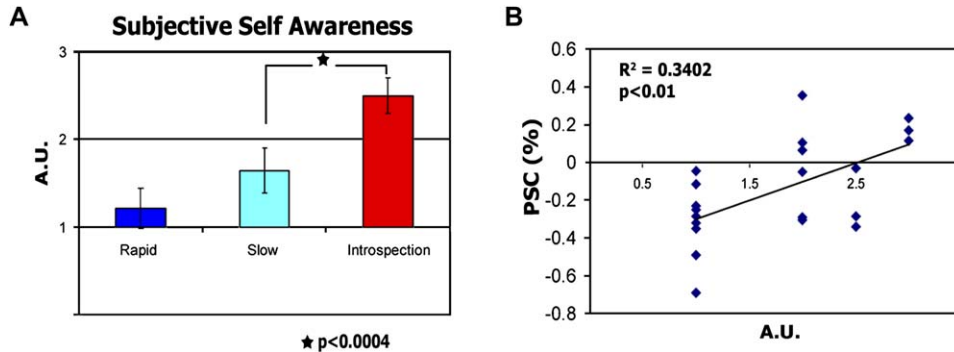


Figure 2. Evaluating Subjective Self-Awareness

(A) Subjective ratings of the level of self-awareness during the three experimental conditions ($n = 7$). Note that the rapid categorization task successfully eliminated subjects' sense of self-awareness. Arbitrary unit scale: 1 = no or negligible sense of self-awareness, 2 = mild level of self-awareness, 3 = strong sense of self-awareness. Error bars, SEM.

(B) Scatter plot showing correlation between subjective self-awareness and SFG activation ($n = 7$). Vertical axis shows the percent signal change (PSC), while the subjective rating of self-awareness is plotted on the horizontal axis (scale, same as in [A]). Each data point represents one condition in one subject. Note the significant positive correlation between the reported level of self-awareness and fMRI activity in the left SFG.

that indeed a high level of self-awareness was experienced during the introspection task, while the rapid categorization virtually abolished any subjective self-awareness experience (Figure 2A; for details about subjective rating, see Experimental Procedures). Averaged data for the nine subjects in the visual scan showed performances of 95% and 98% for rapid and slow categorization, respectively, and 554 ms (SE, ± 10 ms) and 730 ms (SE, ± 25 ms), respectively, for reaction times.

Visual Domain: Mapping Introspection-Related Activity

In order to map introspection-related activity, we compared activity elicited by the introspection task with

that elicited during the slow categorization task during the visual scan. Note that in terms of sensory stimuli and motor output the two conditions were identical. The only difference between the two conditions was in the cognitive task, which changed from pure sensory processing to an introspective task involving both sensory processing and self-related interrogation. Thus, we expect this contrast to highlight self-related areas and areas involved in reflective processes. Figure 3 shows the results of this analysis. The figure depicts multisubject, averaged data, while individual maps are shown in Figure S1 (in the Supplemental Data available with this article online) to provide an estimate of individual variations. We indeed found consistent and

Visual modality

Introspection vs. Slow

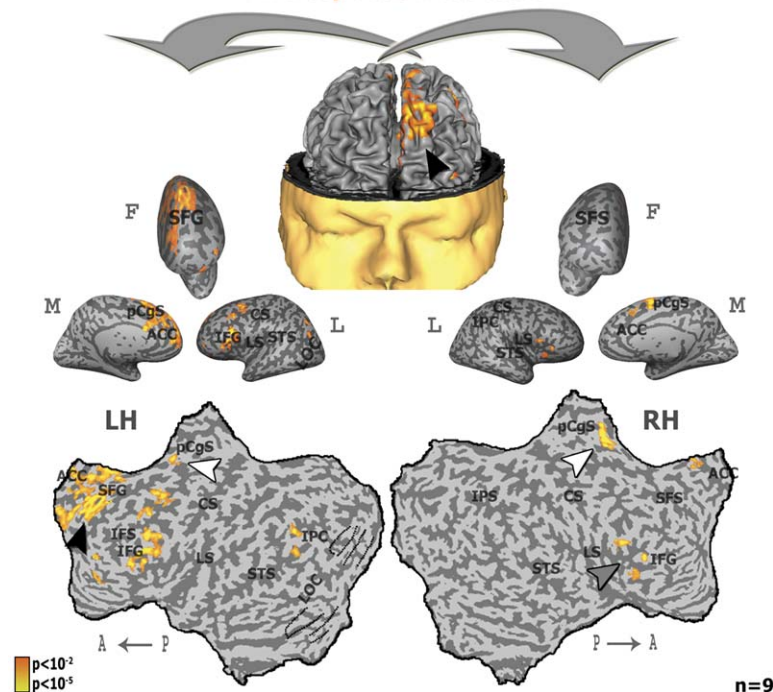
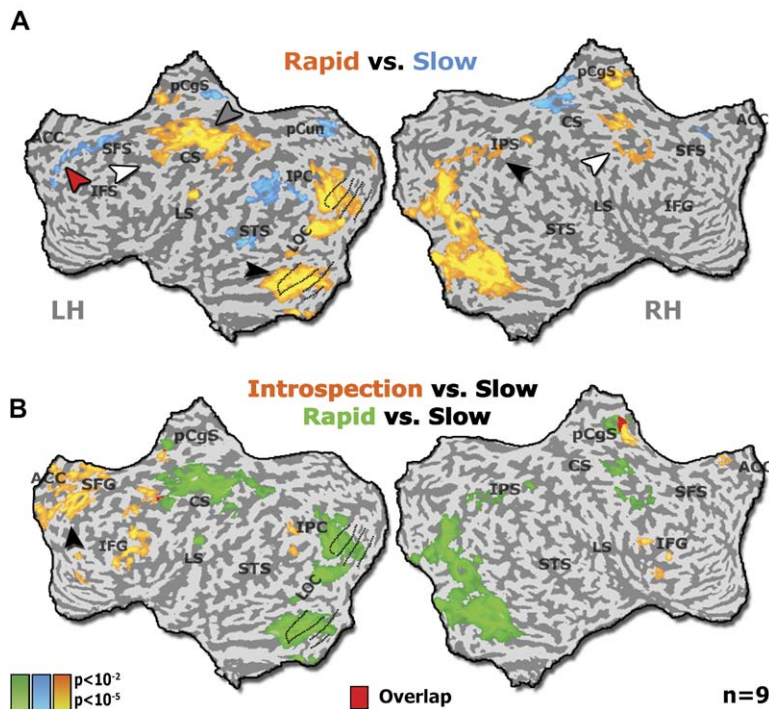


Figure 3. Introspection-Related Activity: Visual Scan

Activity maps for introspection versus slow categorization tasks during the visual scan shown in a folded view of both hemispheres in their anatomical relations (center-top panel), inflated (middle), and unfolded (bottom) formats. Activation map from multisubject ($n = 9$), random-effect GLM analysis. The color scale indicates statistical significance. Main foci, in yellow-orange, were in prefrontal areas and lateralized to the left hemisphere. CS, central sulcus; SFG, superior frontal gyrus; SFS, superior frontal sulcus; ACC, anterior cingulate cortex; pCgS, paracingulate sulcus; STS, superior temporal sulcus; IFG, inferior frontal gyrus; IFS, inferior frontal sulcus; IPS, intraparietal sulcus; IPC, inferior parietal cortex; LS, lateral sulcus; pCun, precuneus; LOC, lateral occipital complex; LH, left hemisphere; RH, right hemisphere; A, anterior; P, posterior; M, medial; L, lateral. Dotted line, estimated retinotopic borders.

Visual modality



significant activations (marked in orange-yellow colors) in a network of areas that were mainly localized in the PFC (for Talairach coordinates, see Table S1). Most prominent activations were found in both medial and lateral aspects of the PFC with clear lateralization to the left hemisphere. Regions selectively activated by the introspection task were found within the superior frontal gyrus (SFG; black arrow) extending medially to the anterior cingulate region and caudally to the paracingulate region; the latter region showed similar activation also in the right hemisphere (white arrow). Additional focus was found in the posterior part of the middle frontal gyrus, just anterior to the precentral sulcus. Finally, bilateral activations were found in the posterior part of the inferior frontal gyrus extending to the anterior insula (gray arrow). In addition to PFC activations, we found a few patches in more posterior locations of the left hemisphere located at the parietotemporal junction (also termed the IPC). No cortical region showed the opposite preference, i.e., significantly higher activations to slow categorization versus introspection.

Visual Domain: Mapping Sensorimotor Processing

In order to reveal the activations related to sensorimotor processing we examined a second contrast—rapid versus slow categorization conditions. Note that here, unlike the previous contrast, the tasks were identical; however, the rate of sensory as well as motor processing was tripled in the rapid condition. We thus expect all cortical regions involved in sensorimotor processing as well as all structures that are activated by task difficulty, working memory, and attentional load to be highlighted.

Figure 4A depicts this pattern of activity on a multisubject map; individual maps are shown in green in Figure S1. Talairach coordinates of major foci are shown

Figure 4. Sensorimotor-Related Activity and Its Relation with Introspection-Related Activity: Visual Scan

Multisubject maps ($n = 9$). (A) Sensorimotor activation revealed by the rapid versus slow categorization conditions, presented on unfolded maps. Yellow-orange regions indicate significant activations for rapid versus slow contrast (rapid > slow) as in left motor and bilateral premotor regions (gray and white arrows), while blue regions indicate the inverse contrast (slow > rapid). Notice the left superior frontal gyrus (red arrows) and posterior superior temporal sulcus. Note that the task (categorization) was identical, while the rate was tripled during rapid compared to slow categorization. (B) Superimposing the introspection and the sensorimotor activation maps. Here, yellow-orange regions show preferential activation for introspection versus slow categorization (introspection > slow), while green regions show preferential activation for rapid versus slow categorization as in (A). Note the striking segregation of the two maps with minimal overlap (red areas). Notation same as in Figure 3.

in Table S2. As can be seen, enhanced activation to the faster stimulus rate (yellow-orange patches) was evident in the entire chain of well-known visual areas along their hierarchical processing, from V1 to LOC (dashed lines) as well as parietal (black arrows) and premotor (white arrows) cortices bilaterally, likely involved in attention and planning motor functions, and finally motor areas (gray arrow) lateralized to the left hemisphere (note that all subjects responded with their right hand).

Here, we also found a set of regions that apparently have manifested an opposite trend—i.e., higher activity during the slow compared to the rapid categorization (blue voxel). These included the posterior cingulate and precuneus sulci and IPC in the left hemisphere. Particularly relevant to the present issue is the large negative focus in the SFG, which was strongly lateralized to the left hemisphere (red arrow). These regions likely correspond to the previously termed “default” brain network (Raichle et al., 2001). It can already be evident from the maps, that the introspection-related regions and sensorimotor ones were largely segregated, with the former mainly associated with PFC regions, while the latter with occipitoparietal and temporal cortices.

To examine in more detail the relationship between these two sets of regions, we superimposed the introspection-related and sensory-related maps. This is shown in Figure 4B for a multisubject map and in Figure S1 for individual data. In these maps, overlap regions are depicted in red. Note the striking segregation of activated regions revealed by these two contrasts—considering the inevitable neuroanatomical blur induced by the multisubject maps, the segregation is quite striking. Small overlap regions appeared in transition zones in the paracingulate region mainly on the right, and in the left precentral sulcus. However, close inspection of

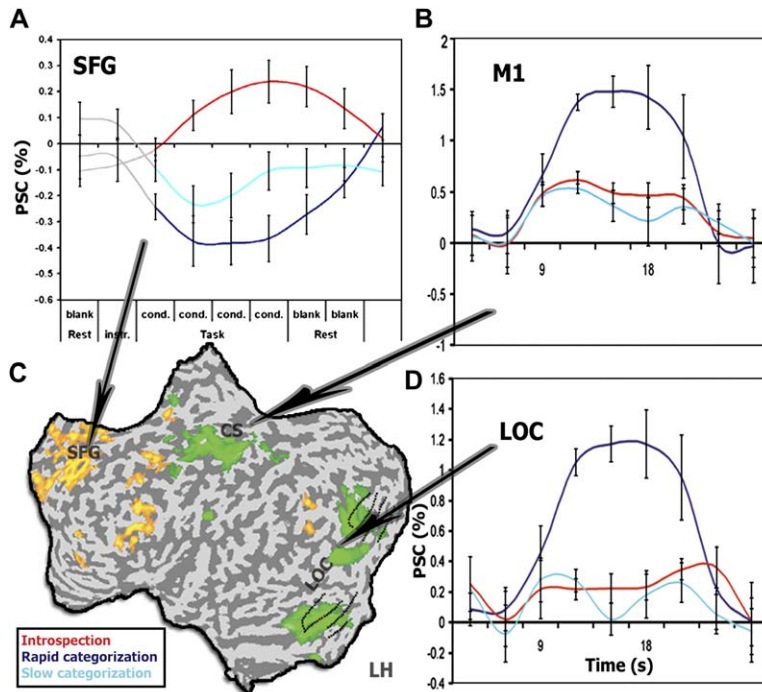


Figure 5. Time Course Analysis in Sensorimotor and Introspection-Related Areas: Visual Scan

Averaged time courses during introspection (red), rapid (dark blue), and slow (light blue) conditions. Data taken from three different ROIs in the left hemisphere (see [Experimental Procedures](#) for ROI definitions). (A) Averaged time courses ($n = 9$) from the SFG. Note the striking difference compared to sensorimotor cortices. Here, only introspection showed a positive (above baseline) response ($p < 0.012$, two-tailed, one-sample Student's t test). (B) The averaged time courses ($n = 8$) sampled from motor cortex (M1) show positive activation in all conditions with marked increase during rapid categorization. (C) Same map as in [Figure 4B](#). (D) Averaged time courses ($n = 8$) from nonretinotopic object areas (LOC); note the similar trend to M1. Error bars, SEM.

the individual maps ([Figure S1](#)) revealed that this overlap was not consistent and was likely due to intersubject variability of individual maps.

Time Course Analysis of Main Foci of Activation

To obtain a more quantitative description of the differential activation patterns, we sampled time courses from representative foci of activity of the left hemisphere (for details about region of interest [ROI] definition, see [Experimental Procedures](#)): (1) primary motor cortex; (2) nonretinotopic object areas including the LOC extending into the posterior fusiform and collateral regions; (3) an introspection-related region in the SFG. The results of this analysis are shown in [Figure 5](#). The respective activation time courses are shown for each ROI, and the respective ROIs are indicated by the arrows leading from the time course to the ROI location on the flat map. Going from posterior to anterior, one can discern first the object-related areas in the non-retinotopic visual cortex ([Figure 5D](#)). In these regions, all conditions resulted in an increase of activity compared to the rest period. However, the rapid categorization task caused a significantly higher activation compared to slow and introspection conditions ($p < 0.001$, two-tailed, paired Student's t test for rapid versus introspection conditions and for rapid versus slow conditions). The same behavior was also noted in primary motor cortex ([Figure 5B](#); $p < 0.001$, two-tailed, paired Student's t test for rapid versus introspection conditions and for rapid versus slow conditions). However, the most critical result of this analysis is presented in cortex strongly associated with introspection—i.e., left SFG ([Figure 5A](#)), inferior frontal cortex, and also small islands in the IPC ([Figure S3](#)). While there are some differences between the various regions, several common effects are apparent in the time courses obtained from these regions: First, introspection led to enhanced activation above baseline

(in SFG, $p < 0.012$, two-tailed, one-sample Student's t test), while both sensory categorization tasks led to inhibitory responses below resting level ($p < 0.006$ and $p < 0.001$, two-tailed, one-sample Student's t test, for slow and rapid conditions, respectively). Second, increasing the speed of sensorimotor processing did not lead to enhanced activation—rather it either was similar or perhaps even led to deeper inactivation.

The results clearly argue against coactivation of self-related cortex during intense sensory processing. While manifesting a pronounced inhibition during sensorimotor tasks, the level of activity in the self-related cortex showed a highly significant positive correlation with the subjective rating of subjects' self-awareness state during the various conditions ([Figure 2B](#)).

How Reproducible Was the Introspection-Related Activity?

While the perceptual categorization task is a well-established paradigm that has been employed in a number of fMRI experiments of object recognition (for a recent review, see, e.g., [Grill-Spector and Malach, 2004](#)), the introspection task is rather novel. Furthermore, compared to object categorization, the introspection task certainly appears to be more loosely defined and multidimensional, and thus may have been subject to idiosyncratic interpretations by different subjects participating in the fMRI experiment. Thus, a potential problem in using this task could be that different individuals will show a highly differentiable activation patterns to this task, making any generalized conclusions quite untenable. To directly examine this problem, we compared how reproducible the activation pattern was during the introspection task compared to the rapid categorization task. To that end, we superimposed all the individual activations during these tasks on one map. The results of this analysis are shown in [Figure 6](#). The activation

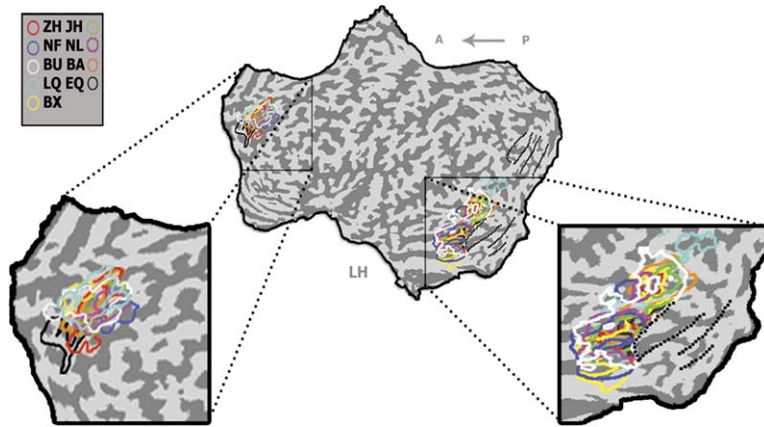


Figure 6. Level of Intersubject Variability in the Introspection- and Sensory-Related Areas in Visual Scan

Borders of cortical areas from nine subjects were superimposed on unfolded hemisphere to assess their intersubject variability during the visual scan. Colored lines represent boundaries of activated regions for each subject. (Right panel) Enlargement of the posterior visual cortex; colored contours indicate boundaries of LOC in individual subjects. Dotted line delimits estimated retinotopic areas. (Left panel) enlargement of the superior frontal gyrus (SFG). Colored contours indicate boundaries of introspection-related activity. Note that the intersubject variability was roughly similar in these two sets of regions. LH, left hemisphere; A, anterior; P, posterior.

boundaries of different individuals are delineated by colored contours. On the right are shown the LOCs of different individuals, and on the left, the self-related areas in the SFG. Note that the intersubject variability was not dramatically different in these two sets of regions.

Are the Results Unimodal?

So far, we have discussed results that were strictly confined to visual processing. To examine whether these results generalize to sensory processing of other modalities, we repeated the same experimental design but this time used the auditory modality. The basic experimental design is shown in Figure 1. Note that it was aimed to be similar to that of the visual modality experiments (for details, see Experimental Procedures). Subjects listened to short musical phrases that were generated by different musical instruments. Again there were three conditions: in the slow categorization task, subjects had to identify whether the sound was of a trumpet versus any other instrument. Rate of presentation was 1 stimulus/3 s, as in the “visual scan.” In the introspection task, stimuli and responses were identical, except that subjects were required, after listening to the stimulus, to indicate how the sound made them feel: positive/negative versus neutral. Finally, in the rapid categorization task, the task was identical to the slow categorization task, but rate of presentation was tripled (1 stimulus/s).

To directly compare the activation during introspection versus sensorimotor processing, we superimposed the two maps. The results are shown in Figure 7 (for de-

tailed maps, see Figure S2). To map the introspection-related activity, we contrasted the introspection versus slow categorization conditions. Similar to the visual domain, these had identical sensorimotor events but differed in the task involved. Figure 7 depicts the regions preferentially activated during the introspection task (yellow-orange voxels). As can be seen, the introspection versus slow categorization tasks showed a remarkably similar activation pattern to that found during the visual introspection task. Patches of activation (marked in orange-yellow colors) were found predominantly in the left PFC, the SFG (black arrow), paracingulate sulcus, and inferior frontal gyrus. Although of less statistical significance, foci of activation were in similar anatomical locations to those found in the visual scan. No significant activations were found for this contrast in the right hemisphere. Some patches showed preferential activation for slow categorization versus introspection, but these were of weak activation and located mainly in posterior brain regions (shown in Figure S2A). Comparing the rapid versus slow categorization conditions (shown in Figure S2B) highlighted, as expected, auditory cortical areas bilaterally and left primary motor regions (green voxels). Also, premotor areas were activated bilaterally with slight lateralization for the right PFC, where activations reached more rostral regions—for example, in the middle frontal gyrus. Note that similar to the visual domain there was a striking segregation of the two activation maps, indicating that in the auditory modality too, the introspection task and the

Auditory modality

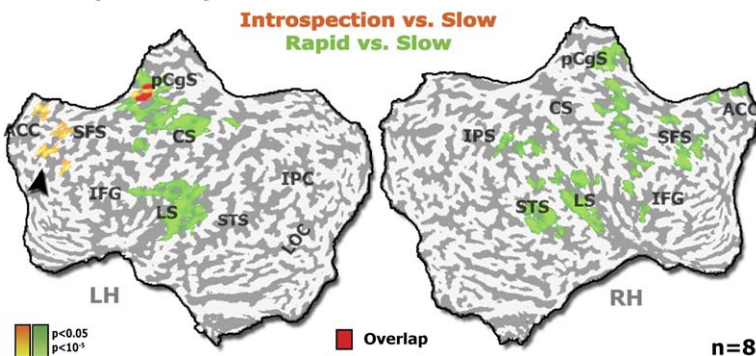


Figure 7. Introspection and Sensorimotor Activations Maps: Auditory Domain

Multisubject ($n = 8$) unfolded maps showing superposition of the introspection and the sensorimotor activations (for detailed maps, see Figure S2). As in the visual domain, note the clear segregation of the two maps with minimal overlap (red areas) mainly in the left paracingulate sulcus. Notations same as in Figure 3.

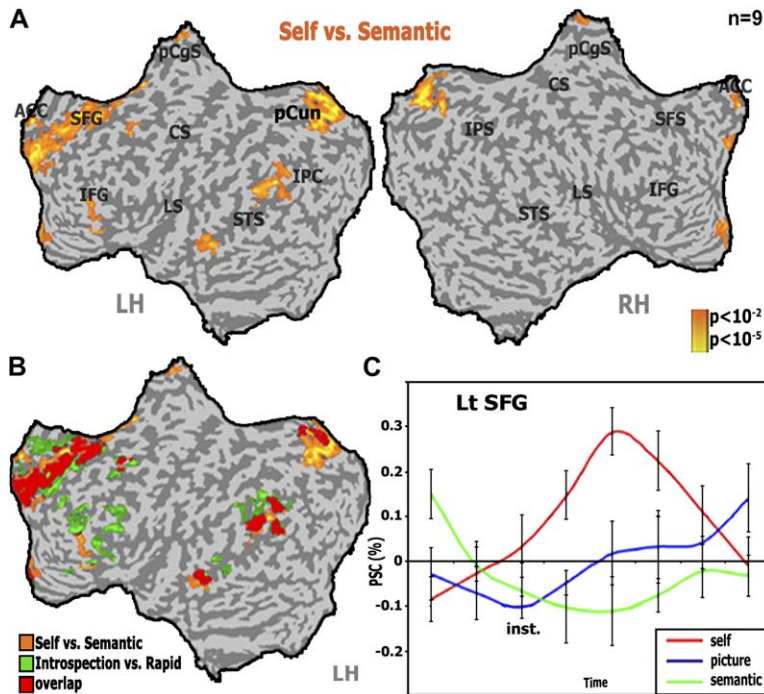


Figure 8. Self-Judgment Control Experiment (A) Multisubject activation map ($n = 9$) for self versus semantic tasks shown in an unfolded view of both hemispheres. Random-effect GLM analysis. The color scale indicates corrected statistical significance. Main foci, in yellow-orange, are present in the left SFG and medial PFC bilaterally. Note foci of activation in posterior cingulate/precuneus and temporoparietal regions. (B) Unfolded view of the left hemisphere. In green, activation map from introspection versus rapid categorization contrast during the visual introspection experiment. In yellow-orange, self versus semantic task, as shown in (A). Red area corresponds to regions that showed significant activation in both experiments. Note the SFG in the PFC and, in the more posterior region, three foci of activity reminiscent of the “default network.” Notations same as in Figure 3. (C) Averaged time course ($n = 9$) sampled from the self-judgment control experiment. Colors denote self (red), semantic (green), and picture (blue) judgment tasks. ROI defined within the SFG using the contrast: introspection versus rapid categorization during the visual introspection experiment. Activation of the self-judgment showed a clear positive response compared to the semantic judgment task, which resulted in inhibitory response. The emotional picture judgment task, although higher than the semantic task, was clearly below the self-judgment. Error bars, SEM.

sensorimotor processing tasks activated mainly non-overlapping territories. Finally, similar to the visual domain, increasing the processing rate did not lead to enhanced activity but showed similar and perhaps even more negative response.

Thus, with regard to the issue of coactivation of self-related regions during intense sensorimotor processing, the results from both the auditory and visual modalities converge in showing a clear segregation between these two sets of areas. Furthermore, increasing the sensorimotor demands failed to simulate the introspection effects.

Possible Involvement of Emotional Processing

When considering the various aspects involved in the introspection task, it is clear that this is a highly complex cognitive state. While the self-reflective aspect was the most outstanding one, there is no doubt that other mental dimensions were engaged as well. A particularly prominent aspect that has been tightly associated with introspection and self-related processes is emotional engagement. Thus, it could be argued that the higher activation we found during introspection may not be due to self-related processes, but rather to enhanced attention or processing of emotional stimuli. To examine this possibility, we conducted a control experiment in which, on the one hand, we attempted to define self-related processes using more neutral stimuli, while on the other hand we used highly emotional stimuli while attempting to minimize the self-related aspects. To that end, we modified a previously reported judgment task used to map self-related areas (Kelley et al., 2002). Subjects

were presented with a set of words and were asked in one condition (self) to judge whether the words applied to themselves and in the other condition (semantic) to judge whether the word was a noun or a verb. We have made a specific attempt to use words which were as emotionally neutral as possible. In the third condition, subjects were presented with highly emotional pictures and were asked to judge whether the pictures were attractive or not (see Experimental Procedures for details).

The results of this control experiment are shown in Figure 8. Figure 8A shows a multisubject ($n = 9$) map showing the contrast self versus semantic judgment. Similar to the introspection test, this contrast highlighted clear activation foci strongly lateralized to the left PFC and localized islands of activity in posterior cortex lateralized around the left IPC and bilateral in the precuneus region. To examine whether these activations corresponded to the regions activated during the introspection task, we superimposed the introspection map and the self-judgment control. The result of this superposition is shown in Figure 8B. Note that a clear-cut overlap can be evident between the two experiments, particularly in the left SFG as well as in the more posterior IPC. Using the introspection experiment to define an external SFG ROI (using the contrast introspection versus rapid categorization), we sampled the activity for the three conditions of self-judgment control experiment. The results are presented in Figure 8C and show a highly significant ($p < 0.002$, two-tailed, paired Student's t test) activation to the self versus semantic judgment task, which resulted in clear inhibitory response,

below the rest baseline. The emotional picture judgment task, although higher than the semantic task, was again clearly below the self-judgment task. These results support the conclusion that the SFG is mediating aspects of self-related, rather than purely emotional, processing.

Discussion

The main outcome of the present study was the finding of a complete segregation between self-related cortical regions, revealed through introspection-related activity, and sensorimotor cortex, revealed through rapid categorization-related activity. Furthermore, rather than showing coactivation, self-related cortex was inhibited during the rapid categorization task (see [Figure 5A](#)) below the rest condition, indicating that sensory processing and self-related representations are actually mutually antagonistic processes. Thus, activity in self-related regions showed a consistent inhibition during sensorimotor processing. Before discussing the possible implications of this finding, we discuss the possible reservations.

Is the Introspective Task Appropriate?

The first obvious reservation is that our method for highlighting self-related cortical regions may have not been appropriate. Indeed, the entire concept of self and its possible cortical representations is still quite a controversial issue ([Keenan et al., 2001](#); [Morin, 2002](#)). This is not surprising, since the nature and attributes of self-related systems are highly complex and still rather ill-defined. Thus, one could argue that the introspection versus slow categorization contrast used here activated mainly regions concerned with emotional processing or with more deliberate contemplative type of thinking rather than true self-related activity.

On the other hand, it could be argued that different self-engaging cognitive tasks could have been more effective in revealing additional self-related representations that were not highlighted in the present experiment and may have different relationships or even coactivated during sensorimotor tasks.

Several lines of evidence suggest that these valid concerns do not apply in the present study. First, comparing the present results to other studies that attempted to map self-related activations revealed a substantial level of consistency across all these studies. Despite the use of a rather wide range of self-related tasks, all these studies converge onto a common network of areas. In particular, all these results share consistently increased activity in medial PFC (BA32) extending laterally to the superior frontal sulcus (BA 8-9-10) ([Schmitz et al., 2004](#); [Johnson et al., 2002](#); [Lane et al., 1997](#); [Frith et al., 1999](#); [Gusnard et al., 2001](#)). Furthermore, our own results, which employed two different self-related tasks—introspection and self-judgments—showed a significant overlap between these tasks in the activity level at the SFG as well as additional PFC areas, which were also related to the subjective rating of self-awareness produced by subjects (see [Figure 2B](#)). Interestingly, these areas show substantial overlap with the “default mode” network of areas ([Raichle et al., 2001](#)), which are intriguingly related to high-level mental functions

such as “theory of mind” and social cognition ([Vogeley and Fink, 2003](#); [Iacoboni et al., 2004](#)).

Could it be that other self-related tasks may engage additional cortical areas not highlighted by the present study? A number of studies, examining self-related activations, most prominently recognition of self-images, reported a right hemisphere bias in the activation patterns ([Keenan et al., 2000](#); [Schmitz et al., 2004](#)) (but see [Turk et al., 2002](#)). Although these reported activations appear to be at homologous locations to the activations reported here, the present results point to left rather than right hemisphere bias. However, close inspection of our activation maps during rapid categorization does not indicate a possibility of overlap between these activations and right prefrontal areas, which were not activated during the rapid sensory categorization task (see [Figure 4A](#)). Furthermore, it should be emphasized that, within the large array of possible self-related cognitive tasks, the ones chosen here, namely sensory emotional introspection and self-judgment, are likely to cover a large spectrum of self-related processes. Indeed, as noted already by [James \(1890\)](#), introspection is the central route by which we reflect upon and report to the outside world about the existence, quality, and fine characteristics of our sensory experiences. Note also that, in the introspection task, both the sensory and motor aspects were identical to the slow categorization task, so all the differential activations we found should have been strictly related to the introspective aspect of the task.

With regards to the possibility that the introspection task was ill defined, and subject to idiosyncratic interpretations by different subjects, our results show that, to the contrary, the activation during this task was no less reproducible across individuals than the more conventional object categorization task (see [Figure 6](#)).

It is important to note that the self-related activations reported here were also compatible with the large body of evidence obtained from neuropsychological literature ([Kolb, 1990](#); [Luria, 1973](#)), in particular the medial wall of the PFC ([Damasio, 1994](#); [Stuss and Anderson, 2004](#)). Thus, our results are substantially compatible with the literature of self-related brain activation.

Finally, although subjective awareness is intimately linked to emotional processing ([Damasio, 1999](#); [Gusnard et al., 2001](#); [Phan et al., 2004](#)), our control experiment in which we chose a self-judgment task involving emotionally neutral words strongly argues against an emotional confound in our results. The fact that the same cortical regions, particularly the left SFG, were activated by both emotional introspection and self-judgment and not by the emotional judgment task ([Figure 8C](#)) strongly supports a self-related rather than emotional attention role for this region.

Variations in Baseline Activity

Unlike sensory and motor cortex, prefrontal, self-related regions showed substantial fluctuations in baseline, “task-negative” activity (e.g., [Figure 5](#)). The source of this effect is unclear at present. One possibility is that it reflects “rebound” effects stemming from the preceding epoch. If such baseline effects persisted into the task period, they may have affected the measured activation level. This factor may be particularly relevant in

assessing whether the inactivation level in prefrontal regions was accentuated by the task demand. However, it should be noted that a relationship between task difficulty and inhibition level has been reported in a number of previous studies of cortical inactivation (e.g., McKiernan et al., 2003).

Relevant Data from Previous Experiments

Supporting data to our present results can be found also in a number of studies that report consistent inactivations in prefrontal cortical areas. Thus, in experiments that were aimed to find self-related activations, Kelley et al. (2002) and Gusnard et al. (2001) also found clear inactivation during sensory categorization functions. Here, we extend these results by showing (1) that the introspection-related activation could not have been explained simply by attentional load that may have been associated with introspection, since increasing the rate of sensorimotor processing failed to mimic the enhanced activation found during introspection; (2) that the inhibitory effects occur during both visual and auditory categorizations; (3) that the self-related results are not limited to emotional introspection but overlap with a completely different self-related task—self-judgment (see Figure 8B).

The inhibition of cortical area by sensory stimulation is also reminiscent to that found in the “default mode” brain network of areas (Raichle et al., 2001), which undergo inactivation during a wide variety of goal-directed cognitive tasks and involve also regions in the precuneus and inferior parietal cortex. What is the significance of these robust inactivations? It is tempting to speculate that such inhibitory effects reflect a global resource allocation network, analogous to the attentional “spotlight” proposed for sensory systems (Crick, 1984), which is responsible for “shutting off” cortical representations not needed for the performance of certain tasks. According to this proposal, the cognitive demands during the rapid object categorization tasks necessitate “turning off” the self-related cortical representations. This inactivation is useful to prevent distracting activity that is not essential to the successful accomplishment of the perceptual tasks.

Broad Implications of the Self-Related Inactivations

As noted in the introduction, the fact that self-related cortical representations become inactive during intense sensory perception bears profound implications to models of subjective awareness. Essentially, these results argue that PFC self-representations are not a necessary element in the emergence of sensory perception. Indeed, it appears that self-related activity is actually shut off during highly demanding sensory tasks.

Thus, the present results clearly argue against the inclusion of self-related representations in the list of ingredients necessary for the emergence of subjective awareness. This interpretation is compatible with a large body of neuropsychological data that clearly show that even extensive PFC lesions do not substantially disrupt the phenomenology of sensory perception (Luria, 1973; Stuss and Benson, 1986). We propose that the role of self-related cortex is not in enabling perceptual awareness, but rather in allowing the individual to reflect upon sensory experiences, to judge their possible sig-

nificance to the self, and, not less importantly for consciousness research, to allow the individual to report about the occurrence of his sensory experience to the outside world.

To conclude, the picture that emerges from the present results is that, during intense perceptual engagement, all neuronal resources are focused on sensory cortex, and the distracting self-related cortex is inactive. Thus, the term “losing yourself” receives here a clear neuronal correlate. This theme has a tantalizing echoing in Eastern philosophies such as Zen teachings, which emphasize the need to enter into a “mindless,” selfless mental state to achieve a true sense of reality (Suzuki, 1964).

Experimental Procedures

Subjects

Nine healthy subjects (five women, ages 22–32, right-handed; Raczkowski et al., 1974) participated in the visual scan and the self-judgment control experiment. Among them, eight participated in the auditory scan. Subjects had normal hearing and normal or corrected-to-normal vision and provided written informed consent. The Tel-Aviv Sourasky Medical Center approved the experimental protocol.

Tasks

Subjects were required to fixate throughout the scan and to perform one of two tasks: categorization and introspection. In the categorization task, subjects were asked to categorize pictures into animal/no-animal categories in the visual scan and into trumpet/no-trumpet categories in the auditory scan (see below). During the introspective task, subjects viewed the images (heard musical clips in auditory scan) and then self-introspected about the emotional response elicited in them by these stimuli and categorized their reaction to the stimuli as high (positive or negative) versus neutral emotional response. Subjects indicated with a single button press their responses after each stimuli presentation with the right hand, using the index finger for animal/trumpet or high-arousal introspects, and the middle finger for no-animal/no-trumpet or neutral introspects. Reaction time and percent correct, where relevant, were examined.

Stimuli

Visual scan: stimuli consisted of colored picture of animals, houses, and objects of various levels of emotional arousal (Phan et al., 2004), including a fixation spot. All pictures ($10^\circ \times 10^\circ$ visual angle) were presented for 200 ms. Auditory scan: stimuli were short (1 s) musical clips sampled from different musical instruments databank (trumpet, piano, organ). Presentation software (Neurobehavioral Systems) was used to deliver the stimuli and record subjects responses; visual stimuli were projected via an LCD projector (Epson MP 7200) onto a tangent screen positioned in front of the subject's forehead and viewed through a tilted mirror; auditory stimuli were delivered via headphones.

Experimental Paradigm

The experiment comprised two 528 s long scans: visual and auditory. Stimuli were shown in 12 s blocks and alternated with 6 s gray field-blanks (see Figure 1). Eight blocks for each of the three conditions were pseudorandomly ordered, for a total of 24 blocks (Figure 1A). Each scan, visual and auditory, consisted of three conditions: introspection and rapid and slow categorization. Slow categorization and introspection conditions included four stimuli in each block (one picture every 3 s), while the rapid categorization condition contained 12 stimuli displayed within each epoch. Thus, the presentation rate was tripled in the rapid categorization so that subjects were both stimulated and had to respond at three times the speed of the slow categorization and introspection conditions. During epochs, stimuli were placed within a background of a grass field that was presented throughout the 12 s of each epoch. During blanks, a uniform gray screen with fixation was presented. Before each block, a letter appeared for 1 s (followed by a grass field screen for 2 s) indicating to the subjects what task to do: “I” for

introspection and “C” for categorization. With the exception of stimulus lengths and ISI, visual and auditory scans were similar in all other aspects.

Self-Judgment Control Experiment

The aim of this blocked design scan was to control for emotional attention as a confound of self-representation. The temporal sequence was similar to the visual and auditory introspection scans. Each condition comprised eight 12 s long epochs followed by a 6 s long fixation condition for a total of 24 pseudorandomly interleaved blocks (total time 528 s). A 1 s instruction shown 3 s prior to each block indicated to the subjects what task to perform. Subjects responded after each stimulus in the same way as in the introspection experiments. The scan consisted of three conditions: self-judgment (“self”), semantic judgment (“semantic”), and emotional picture judgment (“picture”). Subjects were presented with a set of words and were asked in the “self” condition to judge whether the words applied to themselves and in the “semantic” condition to judge whether the words were a noun or a verb. The words were specifically chosen to be as emotionally neutral as possible. One-third of the words were verbs (e.g., swim, study, run), and two-thirds were nouns (e.g., bus, radio, coffee). Four words were presented in each block; each word was shown for 400 ms. During the emotional pictures condition, subjects were presented photographs of high emotional valence and were asked to judge each picture as either of positive (attractive) or negative (repulsive) valence. Pictures were selected from the International Affective Picture System (IAPS; University of Florida) based on normative ratings for valence and arousal; negative (50%) and positive (50%) pictures had valence of <4 and >6, respectively, and arousal between 4 and 6 (for both, on a scale of 1–9; Lang et al., 2005). Positive and negative pictures were equally distributed across the condition. Pictures were similar in their physical properties to those presented in experiment 1 (visual introspection). Each block in the “pictures” condition consisted of nine pictures displayed for 400 ms.

MRI Acquisition

Subjects were scanned on a 1.5 Signa Horizon LX 8.25 GE scanner equipped with a standard birdcage head coil. Blood oxygen level-dependent (BOLD) contrast was obtained with gradient echo echo-planar imaging (EPI) sequence (TR, 3000; TE, 55; flip angle, 90°; field of view, 24 × 24 cm²; matrix size, 80 × 80). The scanned volume included 24 to 27 nearly axial slices of 4 mm thickness and 1 mm gap, so to cover the entire cortical surface of the brain. T1-weighted high-resolution (1.1 × 1.1 mm) anatomical images and a whole brain spoiled gradient (SPGR) sequences were acquired for each subject to allow accurate cortical segmentation and reconstruction, and volume-based statistical analysis. The cortical surface reconstructed from the three-dimensional SPGR scan was then unfolded and flattened. The obtained activation maps were superimposed on the unfolded cortex.

Data Analysis

fMRI data were analyzed with the “BrainVoyager” software package (Brain Innovation, Maastricht, Netherlands) and with complementary in-house software. The cortical surface in a Talairach coordinate system (Talairach and Tournoux, 1988) was reconstructed for each subject from the 3D-spoiled gradient echo scan. The obtained activation maps were superimposed on the unfolded cortex. Preprocessing of functional scans included 3D motion correction and filtering out of low frequencies up to five cycles per experiment (slow drift). Statistical mapping was based on the General Linear Model (Friston, 1995). Our analysis consisted of a multiple regression with a regressor for each condition in the experiment, using a boxcar shape and assuming a hemodynamic lag of 3–6 s. The analysis was performed independently for the time course of each individual voxel. After computing the coefficients for all regressors, we performed a Student’s *t* test between coefficients of different conditions (e.g., introspection versus slow categorization). To obtain the multisubject maps, time series of images of brain volumes for each subject were converted into Talairach space and *z* normalized. The multisubject maps were obtained using a random-effect procedure (Friston et al., 1999). The multisubject functional maps were projected on an inflated or unfolded Talairach normalized brain. Sig-

nificance levels were calculated, taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster. This was accomplished by a Monte Carlo simulation (AlphaSim by B. Douglas Ward), using the combination of individual voxel probability thresholding and minimum cluster size of 6 voxels; the probability of a false positive detection per image was determined from the frequency count of cluster sizes within the entire cortical surface (not including white matter and subnuclei). Color scales indicate the statistical level ranging from *p* < 0.01 (darker colors) up to at least *p* < 0.0001 (brighter colors).

Definitions of ROIs

ROIs were defined on the cortical surface as significant clusters of at least 50 mm² (*p* < 0.05, corrected), and the Talairach coordinates were determined for the center of each ROI. Object-related areas (LOC) were defined using the well-established contrast (object images > texture patterns) in each subject using a separate “localizer” scan (Levy et al., 2001; Hasson et al., 2003; Kourtzi and Kanwisher, 2001). Similarly, retinotopic areas were defined using our standard retinotopic mapping approach in a separate experiment described previously (Levy et al., 2001; Hasson et al., 2003). “External localizer” approach was used to define motor cortex (M1) and was defined according to the rapid > slow categorization contrast in the auditory scan within the vicinity of the left central sulcus. Finally, left SFG and additional areas were defined according to the introspection > categorization (slow and rapid) contrast in the visual scan. Note that those tests provide equal bias for the rapid and slow conditions analysis during the visual scan.

Evaluation of Subjective Self-Awareness

This behavioral experiment was conducted outside of the MRI scanner to allow the evaluation to be conducted immediately following the sensorimotor task. Stimuli and responses were identical to the MRI experiment. However, immediately upon completion of the experiment, subjects were asked to rate their subjective self-awareness for each condition on a 1 to 3 scale. In this scale 1 = no or negligible sense of self-awareness, 2 = mild level of self-awareness, and 3 = strong sense of self-awareness (see Figure 2).

Supplemental Data

The Supplemental Data include three supplemental figures and two supplemental tables and can be found with this article online at <http://www.neuron.org/cgi/content/full/50/2/329/DC1/>.

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