The parietal cortices participate in encoding, short-term memory, and decision-making related to tactile shape

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Rojas-Hortelano E, Concha L, de Lafuente V. The parietal cortices participate in encoding, short-term memory, and decision-making related to tactile shape. *J Neurophysiol* 112: 1894–1902, 2014. First published July 2, 2014; doi:10.1152/jn.00177.2014.—We routinely identify objects with our hands, and the physical attributes of touched objects are often held in short-term memory to aid future decisions. However, the brain structures that selectively process tactile information to encode object shape are not fully identified. In this article we describe the areas within the human cerebral cortex that specialize in encoding, short-term memory, and decision-making related to the shape of objects explored with the hand. We performed event-related functional magnetic resonance imaging in subjects performing a shape discrimination task in which two sequentially presented objects had to be explored to determine whether they had the same shape or not. To control for low-level and nonspecific brain activations, subjects performed a temperature discrimination task in which they compared the temperature of two spheres. Our results show that although a large network of brain structures is engaged in somatosensory processing, it is the areas lining the intraparietal sulcus that selectively participate in encoding, maintaining, and deciding on tactile information related to the shape of objects.

tactile shape; object recognition; short-term memory; decision-making; somatosensory

THE SKIN, MUSCLE, AND JOINT mechanoreceptors of the hand generate streams of sensory information that the brain uses to recognize the objects we touch (DiCarlo et al. 1998; Goodwin and Weat 2004; Johansson and Flanagan 2009; Johansson and Vallbo 1979; Johnson 2001; Mountcastle 2005; Roland and Larsen 1976; Romo and de Lafuente 2012). However, the mechanisms underlying tactile object recognition are not yet fully understood (Hsiao 2008). The core problem in recognition is to understand how objects are identified despite the large variations in sensory information that occur, for example, by changing the orientation of an object or the spatial configuration of the hand grasping that object. Recent evidence suggests the somatosensory system might use encoding strategies similar to those of the visual system, hierarchically representing object features, from points to edges, to surfaces and volumes (Bodegård et al. 2001; Iwamura 1998; Yau et al. 2009, 2013). Unique to the somatosensory system, however, is the close association between the sensory and motor networks that is needed to generate the complex hand movements required to obtain tactile information (Lederman and Klatzky 1987; Pesyna et al. 2011; Thakur et al. 2008). A strong functional relationship thus exists between the motor and somatosensory areas that participate in exploring the shape of objects contacted with the hand, as has been conclusively demonstrated by numerous investigations (Gardner et al. 2007b; Miquée et al. 2008; Reed et al. 2004; Stoeckel et al. 2003). In addition to sensory and motor areas, the association cortices in the parietal lobe have been consistently identified as important nodes in the processing of tactile shape (Binkofski et al. 1999; Bohlhalter et al. 2002; Hömke et al. 2009; Reed et al. 1996; Seitz et al. 1991), with special relevance for somatic sensory encoding (Gardner et al. 2007c; Stoesz et al. 2003; Van Boven et al. 2005), kinesthetic perception (Fiehler et al. 2008), attention (Burton et al. 1999), and hand movements (Chen et al. 2009; Culham and Valyear 2006; Gardner et al. 2007a; Naito and Ehrsson 2006). An important remaining question, however, is whether specific circuits exist within sensory, motor, and association areas that specialize in analyzing the three-dimensional (3D) shape of objects (Bodegård et al. 2001), and if so, how specific these circuits are for the different phases of tactile processing such as sensory encoding, short-term memory, and decision-making (Hartmann et al. 2008; Hernández et al. 2010; Li Hegner et al. 2007; Stoeckel et al. 2004; Zhou and Fuster 1996). To approach these questions we recorded event-related blood oxygen level-dependent (BOLD) signals from subjects performing a shape discrimination task in which they had to decide whether two objects presented sequentially, with a delay period in between, had the same shape or not. After controlling for low-level and nonspecific activations by means of a temperature discrimination task, our results show that the cortical areas lining the intraparietal sulcus (IPS) are key processing nodes that participate in encoding, memory, and decision-making relating to the 3D shape of tactile objects.

MATERIALS AND METHODS

Shape discrimination task. To activate the brain areas that process tactile shape, participants performed a discrimination task in which they had to decide whether two objects, presented sequentially to their right hand, had the same 3D shape or not. Subjects lay supine in the magnetic resonance imaging (MRI) scanner with their eyes covered. On each trial, an experimenter handed them a first object, which they explored with their right hand for 6 s. After a 16-s delay, they were handed a second object, which was also explored for 6 s. At the end of the second-object period, a 6-s delay ensued before the onset of an auditory cue that instructed the subjects to press one of two buttons with their left hand to indicate whether objects had the same 3D shape or not (Fig. 1*A*). The participants had to press one of the two buttons within 2 s after the auditory cue. A 16-s intertrial period elapsed before the next trial was initiated. Subjects were instructed to explore each object continuously for the 6-s period. The start and end of the 6-s exploration periods were controlled by the experimenter; that is, subjects started to explore when they felt the object being placed on their hands and stopped exploring when the object was removed from their hands. Importantly, the experimenter constantly checked that subjects explored the objects continuously throughout this period.

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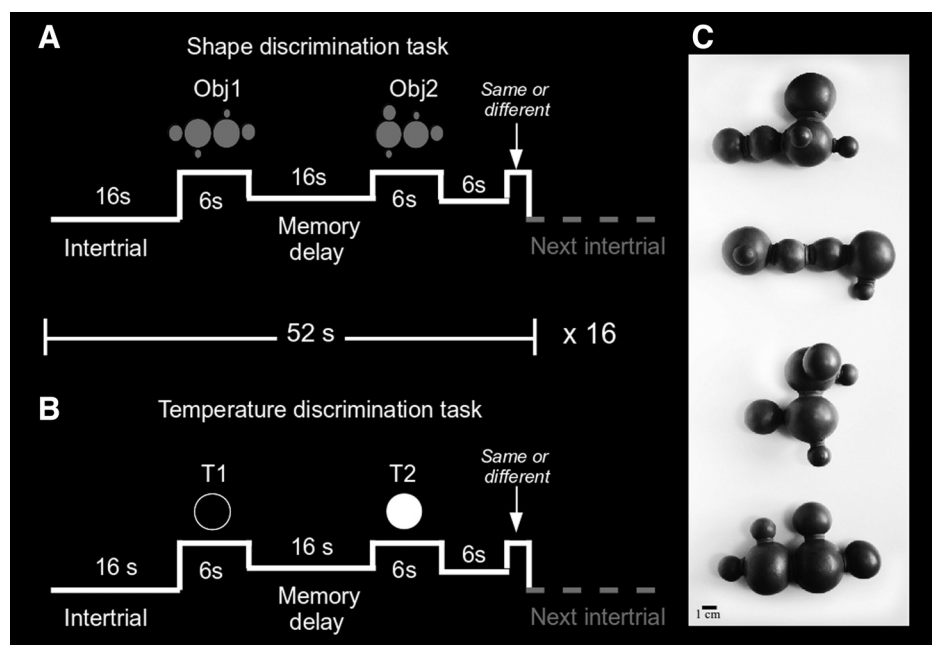
Fig. 1. Discrimination tasks. *A*: shape discrimination task. The 3-dimensional (3D) shape of 2 objects separated by a 16-s memory delay had to be compared to decide if they were different or the same. Subjects communicated their response ("equal" or "different") after a 6-s delay by pressing 1 of 2 buttons with their left hand. *B*: in the control task, the temperature of 2 spheres had to be compared to decide if they were equal or different. Trials were 52 s long, and participants performed 16 trials of each task in the scanner. *C*: tactile objects for the shape task were created by pseudorandomly connecting 2 small, 2 medium, and 2 large spheres (see MATERIALS AND METHODS).

Each trial lasted 52 s; 8 trials with different and 8 trials with equal object pairs were pseudorandomly interleaved, totaling 14 min of task duration. A computer running MATLAB (The MathWorks) and the Psychophysics Toolbox (Brainard 1997; Kleiner et al. 2007; Pelli 1997) was synchronized with the MRI scanner and generated the visual instructions and timing cues that helped the experimenter select and present the objects in a timely manner. This computer also generated the auditory response cue and stored the subjects' choices.

Tactile objects. Twelve different shapes were fabricated from epoxy resin. Each object was built from two large (1.75 cm, 50 g), two medium (1.25 cm, 18 g), and two small (0.75 cm, 4 g) spheres that were assembled according to an algorithm that generated a pseudo-random spatial configuration for each object (Fig. 1*C*). The only constraint was that small spheres were allowed to connect only with one other sphere, the medium spheres with two other spheres, and the large spheres with four other spheres. Objects thus had the same weight and number of constituent elements, and they varied only in the spatial arrangement of those elements. This design prevented the objects from being discriminated from local spatial information and encouraged the subjects to explore the objects to obtain their 3D shape. It is important to note that participants never had visual exposure to the objects and that the discrimination task had to be solved solely from tactile information. Given that 12 objects had to be used in 16 trials that each had 2 object presentations, 8 objects were used 3 times and 4 objects were used 2 times. The objects presented two and three times were chosen randomly and balanced across subjects. To have the same number of "objects equal" and "objects different" types of trial, the first object was selected randomly and the second pseudorandomly.

Temperature discrimination task. Because we sought to identify the brain areas that specialize in the acquisition and processing of tactile object shape, we required an adequate control task to subtract the low-level and nonspecific activations common to tactile tasks. We designed a control task in which participants had to determine whether two spheres had equal or different temperatures (Fig. 1*B*). The temperature task had the same temporal components as the shape task; that is, a first object was presented, followed by a second one after a delay, and finally, the participants had to make a decision. Thus comparable sensory and cognitive elements are present in both tasks: object exploration, memory, and decision-making. We used spheres instead of complex 3D objects because we reasoned that complex tactile forms would have interfered with the shape-processing mech-

anisms that we wanted to isolate. Spheres were at either 22° or 24°C and had the same weight as the objects in the shape task. They were kept within a temperature-controlled container when they were not being handled. Pilot experiments indicated that a 2°C difference at this temperature yielded ~85% correct responses, a performance that is similar to that of the shape task. The number of "temperatures equal" and "temperatures different" types of trials were balanced. It is important to mention that both the control and the shape tasks require high-level functions s working memory and decision-making. These functions, however, are operating on temperature information in the control task rather than on object shape. This design allowed higher order activity that was not exclusively related to shape analysis to be subtracted. As in the shape task, participants were instructed to move their fingers during each 6-s exploration period. The order of temperature and shape tasks was balanced across subjects. Before the imaging session, subjects underwent two training sessions in which they became familiar with the shape and temperature discrimination tasks, and they achieved performance levels significantly above chance.

Subjects and image acquisition. Nineteen right-handed subjects (10 women, age range 22–29 yr) underwent functional magnetic resonance imaging (fMRI) on a 3-T Philips Achieva TX scanner (Best, The Netherlands) using an echo planar imaging gradient echo (EPI-GRE) sequence with a repetition time (TR) of 2 s and echo time (TE) of 27 ms. Functional volumes consisted of 32 axial slices covering the whole brain with a voxel resolution of $2 \times 2 \times 3.5$ mm^3. For each task (shape and temperature) 430 volumes were acquired with a 5-min break between tasks. An anatomic T1-weighted image with a resolution of $1 \times 1 \times 1$ mm^3 was also acquired for registration purposes. Total time within the scanner was 33 min. Data from 4 subjects (3 women) were discarded due to motion artifacts or performance level below 70% correct responses on either task. Subjects gave written consent and were paid for their time. Experimental procedures were in accordance with the Declaration of Helsinki and approved by the institutional Bioethics Committee.

Data processing. Imaging data was analyzed with FEAT (fMRI Expert Analysis Tool) version 5.98, a part of FSL (FMRIB's Software Library; www.fmrib.ox.ac.uk/fsl). Images were subjected to motion correction, temporal high-pass filtering (0.01 Hz), and spatial smoothing (5-mm full width at half-maximum Gaussian filter). The structural image was coregistered to an average functional image using a rigid body transformation, and to the FSL MNI152 atlas using an affine

transformation with 12 degrees of freedom. Correction for multiple comparisons was performed according to Gaussian random field theory (Worsley et al. 1999), and clusters of significant differences (z-threshold = 2.5; $P < 0.01$) are reported in MNI152 coordinates. Data were analyzed by using the general linear model after convolving the experimental paradigm with a canonical hemodynamic response function approximated by a gamma function. The shape and temperature discrimination tasks were divided into five stages each corresponding to a separate regressor in the analysis: *1*) object presentation, *2*) memory delay, *3*) second object presentation, *4*) second delay, and *5*) button press. For the analysis shown in Fig. 5*B* we used a single regressor that included the complete discrimination trial, from the presentation of the first object up to the behavioral response. The intertrial interval was used as baseline. First, each stage was compared with the intertrial interval to identify brain regions showing metabolic activity above baseline; then, to subtract low-level sensorimotor and nonspecific cognitive components, each stage of the shape task was compared with its homologous stage in the temperature task (Shape > Temp). The reverse contrasts were also calculated (Temp > Shape) but resulted in no significant activations, as discussed in RESULTS. The regressors corresponding to the second delay and to the button press also failed to reveal activations above those of the control task. This article thus focuses on the activity associated with the first three regressors (first object presentation, memory, and second object presentation).

RESULTS

Behavior. Subjects performed the shape and temperature discrimination tasks significantly above chance and, importantly, with comparable accuracy (86.3% shape task, 87.5% temperature task, $P = 0.76$, 2-proportion z-test; 236 and 237 total trials, respectively). The similar performance across tasks indicates similar demands in cognitive processes such as attention and memory load, and it validates the temperature task as an adequate control. The behavioral results also show that in

the shape discrimination task subjects tended to answer "objects different" more frequently than "objects equal" (55.1 and 44.9% of trials, respectively, $P = 0.024$, 2-proportion z-test; 236 total trials). This asymmetry was not present in the temperature discrimination task (50.2% "temperatures different", 49.8% "temperatures equal", $P = 0.93$, 2-proportion z-test; 237 total trials), so it is not readily explained by a simple response bias. Instead, it is likely that this asymmetry stems from the difficulty inherent in recognizing complex tactile objects with which the subjects have little previous experience. Given that objects were presented in random orientations, the asymmetry suggests that the same object presented in different orientations could be mistaken for different objects.

Activity during first object exploration. Subjects explored the first object with their right hand for 6 s. This recruited numerous brain areas that increased their metabolic activity significantly above baseline (BL), in both the shape and the temperature tasks (Fig. 2*A*). Compared with baseline (Shape > BL and Temp > BL), tactile exploration of the first object strongly activated parietal, sensory, motor, and premotor areas in the left hemisphere, contralateral to the stimulated hand. The shape task, however, also engaged structures in the ipsilateral hemisphere not activated by the temperature task. The additional areas recruited by the shape task were revealed by the contrast Shape > Temp, and they included area 3b and the primary motor cortex in the ipsilateral hemisphere, as well as the putamen, calcarine, premotor, and intraparietal cortices bilaterally (Fig. 2*B*). These results highlight the interplay between the sensory and motor circuits that is needed to explore an object to obtain its 3D shape. The fact that these sensory-motor areas remain active even after motor and sensory activity is controlled for suggests that they contain neuronal circuits specialized in obtaining the 3D arrangement of objects explored through the sense of touch. It is important to
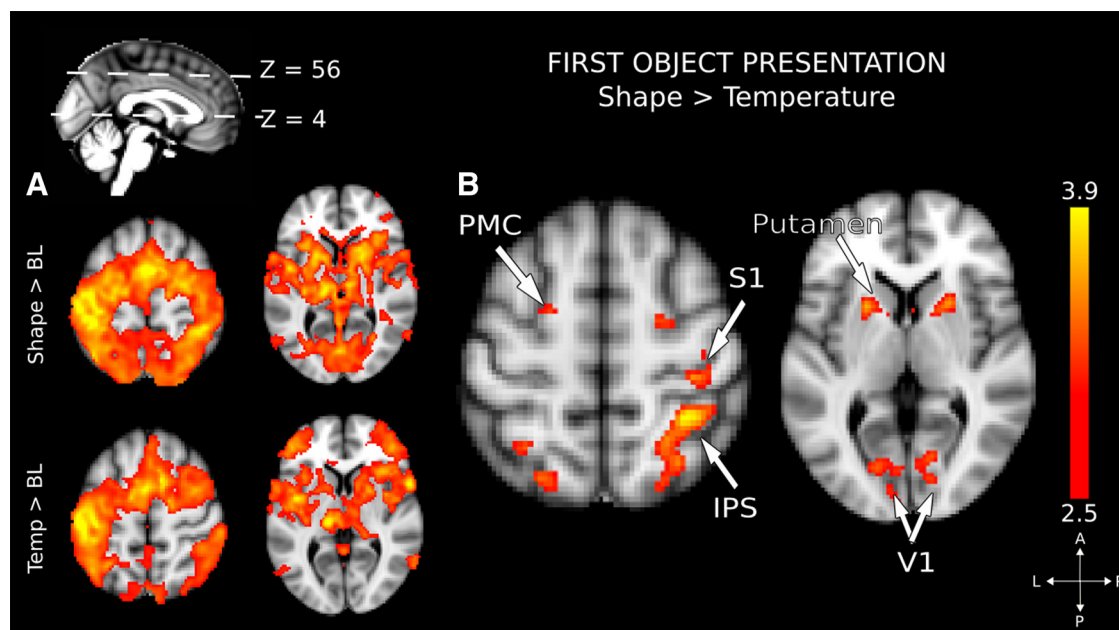

Fig. 2. Activation maps elicited by exploration of the first object. *A*: activity with respect to baseline (BL) for the shape (Shape > BL) and temperature tasks (Temp > BL). The *Z* levels of the coronal slices are shown in the *inset* (*top left*). *B*: the contrast Shape > Temp reveals the areas selectively involved in exploring and encoding the 3D shape of the first tactile object. Color scale indicates *z* values. IPS, intraparietal sulcus; PMC, premotor cortex; S1, primary somatosensory cortex; V1, primary visual cortex. In Figs. 2–5, statistical parametric maps (color) are overlaid on the MNI152 standard brain (grayscale); coordinates are given in mm according to such anatomic space.

note that although the activation in the control task was stronger in the hemisphere contralateral to the stimulated hand, the exploration of object shape bilaterally engaged the somatosensory, motor, premotor and parietal areas (Peltier et al. 2007).

We also observed significant activation of the primary visual cortex, and this activity was selective for the shape task (Fig. 2*B*). The fact that the temperature task failed to produce significant activity in the visual cortex suggests that only tasks that require obtaining the 3D shape of an object from tactile information involve mental imagery, an observation that is consistent with previous reports (Hadjikhani and Roland 1998; Peltier et al. 2007). The contrast Temp > Shape did not reveal significant voxels, indicating that manipulation of an object to encode its temperature activates only a subset of those areas recruited for exploring and encoding its 3D shape.

Working memory for tactile shape. The absence of sensory stimulation and hand movements during the delay separating the presentation of the two objects makes this period an ideal window in which to identify the brain circuits involved in short-term memory of the 3D shape of tactile objects. To solve the task, subjects maintained the shape of the first object in short-term memory, as evidenced by their performance levels that were significantly above chance (see RESULTS, *Behavior*). A number of areas are known to participate in maintaining sensory information that is used to guide behavior, the prefron-

tal cortex (PFC) being one of the most studied (Funahashi et al. 1989; Fuster 2008; Miller et al. 1996). Our results show that, compared with baseline (Mem Obj > BL and Mem Temp > BL), the PFC is active during the delay period separating the presentation of the two objects (Fig. 3*A*). This activation, however, was present in both tasks, suggesting that the PFC might be part of a general working memory network that does not contain specialized circuits for the maintenance of tactile shape. At least to the spatial resolution of our fMRI images (see MATERIALS AND METHODS), our findings indicate that the PFC does not use different neuronal populations to maintain temperature and shape information.

Additional areas that participate in working memory, in both tasks, include the premotor and the lateral parietal cortices. Figure 3*A* also shows that maintaining a memory trace of tactile objects strongly engages the parietal cortex bilaterally. This is clearly demonstrated in the activity elicited by the shape task relative to baseline (Shape > BL). The temperature task also revealed smaller but significant clusters in the parietal cortex (Temp > BL).

To identify the areas selectively engaged in maintaining the working memory of tactile object shape, we performed the contrast Shape > Temp for the delay period separating the object pairs (Fig. 3*B*). This contrast revealed that only the areas in the posterior parietal cortices are specifically engaged in maintaining the short term memory of an object's shape. To corroborate elevated activity throughout the delay, Fig. 3*C*
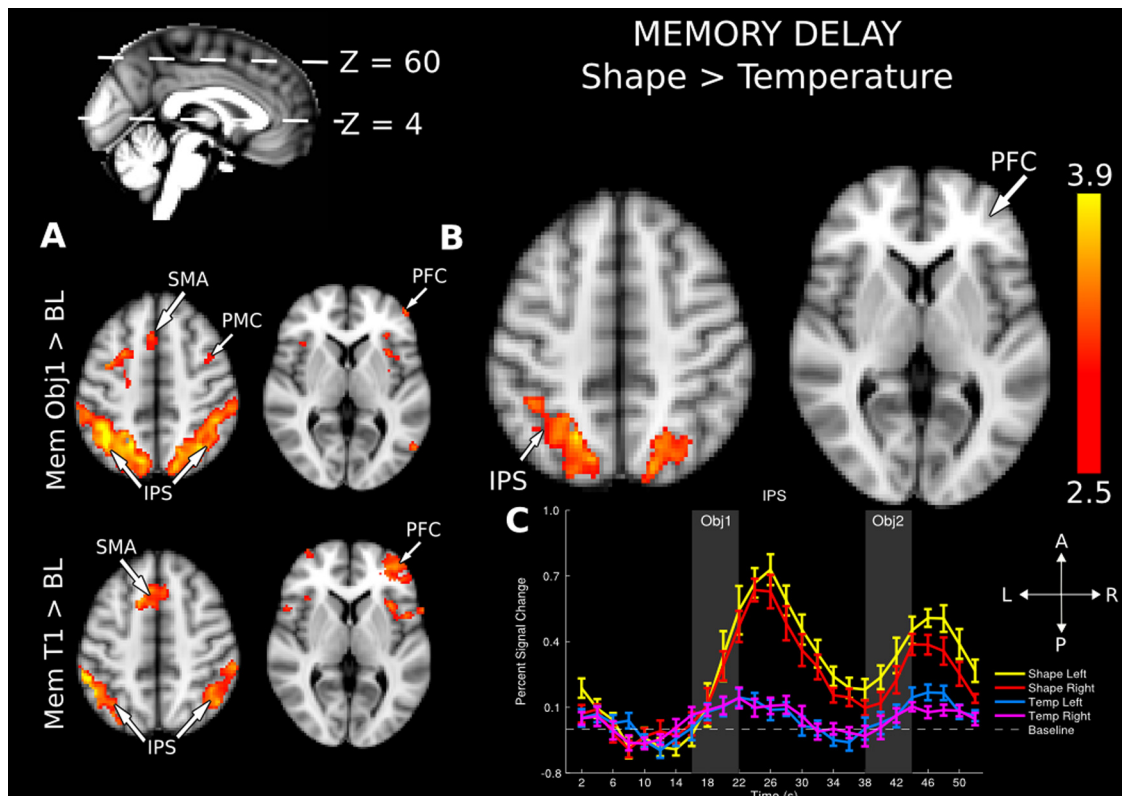

Fig. 3. Activation maps observed during the working memory period. *A*: activity with respect to BL for the memory of shape (Mem Obj1 > BL) and memory of temperature (Mem T1 > BL). The *Z* levels of the coronal slices are shown in the *inset* (*top left*). *B*: the areas selectively involved in maintaining the 3D shape of tactile objects are shown in the contrast Shape > Temp. Note the strong delay activity in the parietal cortices and the absence of shape-selective prefrontal cortex (PFC) activation. Color scale indicates *z* values. *C*: time course of blood oxygen level-dependent (BOLD) activity in the left and right parietal cortices for the shape and temperature tasks. Shaded areas mark the presentation of the first (Obj1) and second objects (Obj2). Error bars indicate SE; $n = 15$ subjects. Voxel coordinates from which maximum activity is plotted are $-20/-62/48$ and $22/-62/42$ for the left and right parietal cortices, respectively. SMA, supplementary motor area.

shows the time course of BOLD activity in the shape and temperature tasks.

Activity during second object exploration. While exploring the second object, subjects must obtain its shape and compare it against the shape of the first object they maintained in working memory. This comparison gives rise to a decision about the two objects being different or the same. Thus, in addition to the mechanisms of exploration and shape encoding that are active in both object presentations, presentation of the second object additionally engages decision-making processes such as object comparison and the selection of a behavioral response to communicate the decision. To examine the brain areas that participate in these processes, we contrasted the activity elicited by the second object (Obj2 > BL; Fig. 4A) against the activity observed during examination of the first object (Obj1 > BL; Fig. 4A). The results of this contrast (Obj2 > Obj1) show that comparing the shape of two objects and generating a decision about whether they are different or the same recruits a network of frontoparietal areas that include the medial premotor, the right ventrolateral PFC, and the parietal cortices bilaterally (Fig. 4B). The reverse contrast (Obj1 > Obj2) yielded a single significant cluster located within the right supplementary motor area (not shown).

Finally, to evaluate how specific these activations are for the shape task, we contrasted the activity elicited by the second object of the shape and temperature tasks (Obj2 > Temp2; Fig. 4C). The results show that only the left premotor and the bilateral parietal cortices are specifically engaged in the decision-making processes of the shape task (Fig. 4C). The PFC activity did not survive the contrast against the control task, suggesting that although recruited for decision-making, it does not contain circuits selective for tactile shape decisions. The reverse contrast (Temp2 > Obj2; not shown) failed to reveal any significant activation, indicating that comparing and deciding about the temperature of two objects recruits only a

subset of the areas required for decision-making related to the shape of objects.

It is important to note that the decision about the shape of the objects being equal or different can initiate as soon as the second object is presented. In fact, the hand movements used to explore the second object could be directed not to obtain its general shape but to obtain information to directly evaluate whether the objects are different or the same. However, it is also possible that subjects could be delaying the decision up until the end of the second object period, or even delaying it into the 6-s waiting period before the button press. To test this, we analyzed the 6-s waiting period that followed the presentation of second object (Fig. 1A). The analysis failed to detect significant clusters in the contrast (waiting period > Obj2), indicating that there is no additional activity in the waiting period compared with the second object presentation. This result suggests that the decision-making process starts as soon as the second object is presented and that this decision activity is maintained throughout the waiting period before the button press.

The areas lining the IPS participate in the three phases of the discrimination task. Our previous analyses showed that each stage of the discrimination task activates a unique set of brain areas. However, it must be noted that the areas lining the IPS are recruited throughout the task for encoding, maintaining in memory, and deciding on the shape of tactile objects. To explicitly show this, we carried a superposition in which we labeled those voxels that were significantly active across the three phases of the discrimination task (Fig. 5A). This conjunction map was statistically validated by performing a contrast in which the three phases of the discrimination task were compared against the three phases of the temperature task: [(Obj1 + Mem Obj + Obj2) > BL] > [(Temp1 + Mem Temp + Temp2) > BL]. This analysis, akin to a block design, does not separate the different components of the task but answers the

Fig. 4. Activation maps observed during exploration of the second object. *A*: activity with respect to BL for the objects in the shape [first object, Obj1 > BL (same as in Fig. 2A); second object, Obj2 > BL] and temperature tasks (second temperature, Temp2 > BL). The Z levels of the coronal slices are shown in the *inset* (*top left*). *B*: the areas engaged by the decision process in the shape task were revealed by the contrast Obj2 > Obj1. *C*: the contrast Obj2 > Temp2 revealed that although the PFC participates in decision-making, this activity is not specific for the shape task. The left medial PMC and parietal cortices, bilaterally, are engaged by decisions involving tactile object shape. mPFC, dlPFC, and vlPFC, medial, dorsolateral and ventrolateral prefrontal cortex, respectively.
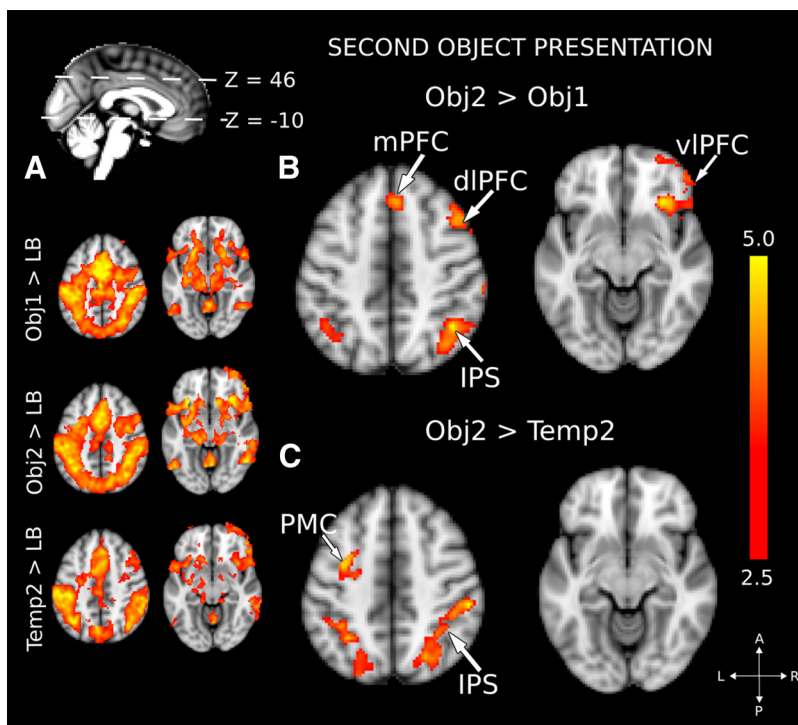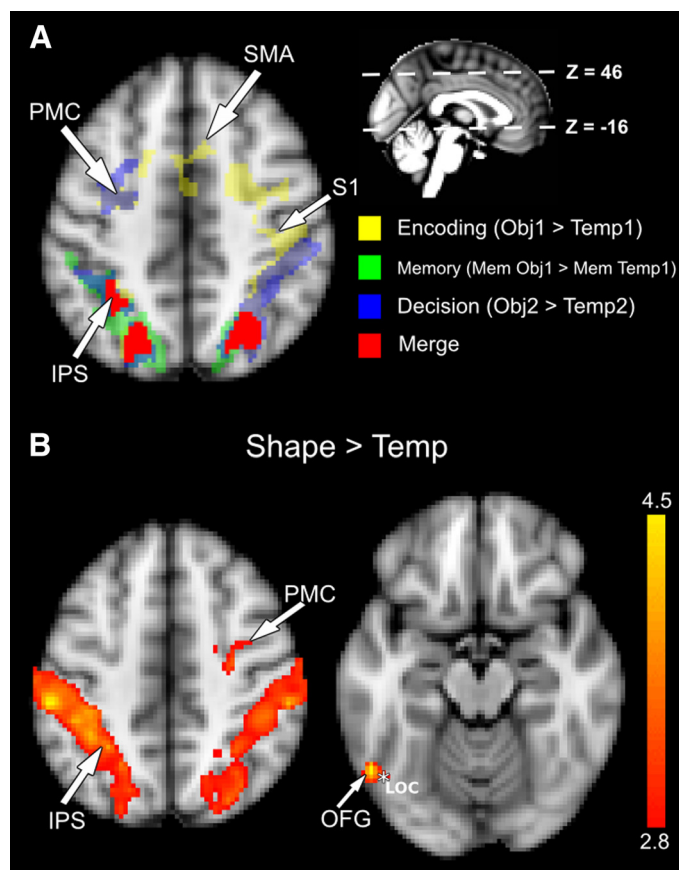
Fig. 5. Superposition of the activity maps observed during each phase of the discrimination task. *A*: although different networks are recruited by the different phases of the task, the cortices lining the intraparietal sulcus participate in all 3 phases: encoding (yellow), memory (green), and decision-making (blue), as indicated by the red voxels. *B*: block-design analysis comparing the shape task against the temperature task: [(Obj1 + Mem Obj + Obj2) > BL] > [(Temp1 + Mem Temp + Temp2) > BL]. The activation map includes the areas around the IPS, with additional clusters in the right PMC and the left occipital fusiform gyrus (OFG). The OFG cluster partially overlaps with the lateral occipital complex (LOC), an area that has been shown to code visually or tactually explored object shape (asterisk indicates the LOC coordinates reported in Amedi et al. 2001, 2002).

question of which areas are active throughout the complete task. The results confirm bilateral activation clusters that include the areas around the IPS (Fig. 5*B*), with an additional cluster in the right premotor cortex and the left occipital fusiform gyrus (OFG). The cluster in OFG partially overlaps the location of the lateral occipital complex (LOC), an area that has been shown to be activated by visual and tactile shapes (Amedi et al. 2001, 2002).

DISCUSSION

Our results show that although each stage of the discrimination task activates a unique set of brain areas, the areas lining the IPS are recruited throughout the task for encoding, maintaining in memory, and deciding on the shape of tactile objects explored with the hand (Fig. 5, Table 1). In addition to the IPS areas that are active across all phases, tactile exploration recruited the motor, premotor, somatosensory, and primary visual cortex (Fig. 2*B*), and the phase of decision-making additionally recruited the prefrontal and medial premotor cortices (Fig. 4*C*). It is important to note that the decision-making

process includes a memory retrieval mechanism that allows comparison of the first and second objects. It has been shown that previously active networks can be reactivated at the end of a delay period (Shulman et al. 2002). It is possible that, as part of the decision process, a reactivation of the network encoding the shape of the first object could be occurring during the presentation of the second object. In the discrimination task we used, subjects had to explore an object with their right hand, hold its shape in short-term memory, and then compare it against a second object to determine whether the two had the same shape or not. Importantly, we contrasted the BOLD activity in the shape task against the activity elicited by a control task that had the same exploration, memory, and comparison components, in which subjects had to determine whether two spheres had the same temperature or not. The temperature task not only controlled for low-level sensory and motor processes but also accounted for nonspecific higher cognitive functions such as memory and decision-making. The use of this control task allowed us to identify the parietal cortices as fundamental for the gathering and processing of somatosensory information regarding the 3D shape of objects explored with the hand.

Newman et al. (2005) showed that areas around the IPS are recruited when subjects are asked to mentally evaluate the geometric properties of objects. However, the visual imagery task used by Newman et al. evaluated cognitive processes different from those required in our shape comparison task. The fact that both tasks recruit areas around the IPS is an interesting finding that further supports the notion that the IPS is a key node in tactile shape processing.

As has been found consistently in previous experiments, the tactile exploration of objects activated the visual cortex (Deibert et al. 1999; James et al. 2002; Zangaladze et al. 1999). Our results now demonstrate that this activation is selective for tactile tasks that require acquiring the 3D shape of an object. The participation of the visual cortex in the encoding of tactile shape suggests that subjects could be using visual imagery to translate somatic sensory information into a visual representation of the touched object (Newman et al. 2005). This activation was not sustained during the memory period, and unlike previous work that showed reactivation of visual cortices during a memory retrieval process (Wheeler et al. 2006), we did not observe V1 activity during the presentation of the second object.

Our block-design analysis (Fig. 5*B*), in which all phases of the shape task were compared with all phases of the temperature task, revealed a cluster of activity that partially overlaps the LOC, an area that represents the shape of objects either seen or explored with the hand (Amedi et al. 2001, 2002). Thus, although we were not able to pinpoint the phase of the task in which LOC becomes active, our results do indicate that LOC participates in tactile shape processing. Previous research by Fiehler and colleagues (2008, 2009) found that LOC activity correlated with the complexity of kinesthetically defined shapes, but only during the phase of encoding.

The absence of sensory input and motor actions during the delay that separates the two objects make this period an ideal window in which to study the brain areas selectively engaged in maintaining the 3D shape of touched objects in short-term memory (Kaas et al. 2007; Stoeckel et al. 2003). The results show that despite also being a tactile task, the temperature task

Table 1. *Location of activity clusters in the 3 stages of the discrimination task*

Task Stage	Functional Regions	Anatomic Localization	Coordinates			Z Value
			x	y	z	
First object (Obj1 > T1)	Dorsal premotor cortex L	Superior frontal gyrus	−14	−12	68	3.3
	Dorsal premotor cortex R	Superior frontal gyrus	24	−6	62	3.7
	Cingulate motor area	Cingulate cortex	4	6	32	3.7
	S1 R	Postcentral gyrus	36	−28	56	3.4
	Intraparietal sulcus L	Intraparietal sulcus	−22	−68	54	3.3
	Intraparietal sulcus R	Intraparietal sulcus	40	−38	50	3.7
	Precuneus L	Precuneal limiting sulcus	−24	−68	42	3.2
	Precuneus R	Precuneal limiting sulcus	30	−60	44	3.9
	V1	Calcarine fissure	12	−84	0	3.2
	Globus pallidus L	Globus pallidus	−22	10	2	3.5
	Globus pallidus R	Globus pallidus	24	12	2	3.5
Memory (Mem Obj1 > Mem T1)	Intraparietal sulcus L	Intraparietal sulcus	−20	−62	48	3.9
	Intraparietal sulcus R	Intraparietal sulcus	22	−62	42	3.4
Decision-making (Obj2 > T2)	Premotor cortex L	Superior frontal gyrus	−34	−2	46	3.9
	Intraparietal sulcus L	Intraparietal sulcus	−36	−52	54	3.5
	Intraparietal sulcus R	Intraparietal sulcus	38	−44	54	4.1

Locations of activity clusters in the 3 stages of the discrimination task were obtained by contrasting the shape and temperature tasks (Shape > Temp; see text for details). Coordinates are given in mm in MNI152 standard space and indicate the location of each cluster's peak significance. L, left; R, right; S1, primary somatosensory cortex; V1, primary visual cortex.

did not engage the parietal cortices as strongly as the tactile shape task. In fact, no significant voxels were identified in the contrast Temp > Shape (not shown), indicating that keeping temperature information in short-term memory does not engage areas in addition to those encoding shape information.

The use of different objects for the shape and temperature tasks could be viewed as a potential drawback in our study. This is because although subjects continuously moved their hands over both kinds of objects, the elaborate 3D configuration of objects in the shape task is likely to require more complex exploratory hand movements and thus could engage different motor plans than those required to sense the temperature of spheres. We decided not to use complex shapes for the temperature task because they could have masked the same processes of shape encoding that we wanted to identify with the shape task. However, due to the use of spheres in the control task, it is important to note that the activation map elicited by the complex objects could also be reflecting the planning and execution of the motor commands needed to obtain the 3D shape of the touched objects. The bilateral putamen activation that we observed during the presentation of the first object might be related to these exploratory motor plans. The activity in ipsilateral primary motor and somatosensory cortices did not differ significantly between the shape and temperature task, suggesting that at least at the most basic processing level, hand movements and sensory stimulation were comparable across tasks. However, it is possible that differences in the complexity of preparation and execution of the exploratory hand movements in the shape and temperature tasks (Drewing 2012; Kaim and Drewing 2010; Lederman and Klatzky 1987) could have more strongly engaged central processing areas such as those around the IPS (Fiehler et al. 2008, 2009; Murata et al. 1996; Singhal et al. 2013). We think this indicates that in a tactile recognition task, the sensory information is tightly woven to the hand movements used to obtain that information and that both processes might be represented within the same cortical circuits.

Another possible concern is that the number of shape alternatives is greater than the number of temperature alternatives;

that is, we used 12 different shapes but only 2 temperatures. This could potentially introduce differences in terms of memory load and decision-making across tasks. It must be noted, however, that behavioral performance is similar in both tasks ($P = 0.76$; see RESULTS, *Behavior*). This indicates that in terms of difficulty, the tasks are comparable. We speculate that differences between tasks in terms of memory load or decision-making would have been reflected in the behavioral performance. Instead, the behavioral results suggest that the temperature difference that we selected was as difficult to compare as the numerous shape combinations.

The behavioral results show that subjects tended to respond "objects different" more often than "objects equal" and that this asymmetry was present only in the shape task. This speaks to the difficulty in recognizing complex tactile objects for which the orientation in which they are presented is randomly changed. However, how changes in orientation affect recognition performance needs a more detailed study. We compared the brain activity of hit and error trials but failed to detect any difference between these trials. This suggests that errors did not arise from distractions or from other processes different from those of successful object comparison.

Relative to baseline, the temperature task strongly activated the hemisphere contralateral to the stimulated hand (Fig. 2*A*). The shape task, however, recruited the ipsilateral hemisphere as well, demonstrating that shape processing involves the parietal cortices from both hemispheres (Fig. 2, *A* and *B*). Future experiments are needed to determine whether this pattern holds if object exploration is performed with the left hand.

Its large receptive fields and sensitivity to postural signals make the second somatosensory cortex (SII) the first cortical node with the capacity to code the 3D shape of tactile objects (Hsiao 2008). Our results, however, do not include SII as an area exclusively related to shape processing. SII was similarly active in the shape and temperature tasks. This does not imply that SII is not important for shape processing but only indicates that it is equally engaged in other tactile tasks.

The participation of the parietal cortices in tactile shape recognition had been consistently demonstrated (Amedi et al.

2001, 2002; Binkofski et al. 1999; Bohlhalter et al. 2002; Grefkes et al. 2002; Hömke et al. 2009; Miquée et al. 2008; Peltier et al. 2007; Reed et al. 1996; Seitz et al. 1991). Our study contributes to that important previous research by separately analyzing the phases of sensory encoding, short-term memory, and decision-making and contrasting these processes against a control task that had the same cognitive components. Our results demonstrate that although a large number of cortical areas are recruited by the different stages of these tasks, it is the parietal cortices lining the IPS that selectively participate in encoding, maintaining, and deciding about the 3D shape of objects explored with the sense of touch.

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GRANTS

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

E.R.-H., L.C., and V.d.L. conception and design of research; E.R.-H., L.C., and V.d.L. performed experiments; E.R.-H. and L.C. analyzed data; E.R.-H., L.C., and V.d.L. interpreted results of experiments; E.R.-H. prepared figures; E.R.-H., L.C., and V.d.L. approved final version of manuscript; L.C. and V.d.L. edited and revised manuscript; V.d.L. drafted manuscript.

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