The Human Dorsal Stream Adapts to Real Actions and 3D Shape Processing: A Functional Magnetic Resonance Imaging Study

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INTRODUCTION

Experience-dependent changes in the functional magnetic resonance imaging (fMRI) signal have been recently used not only to investigate the neural bases of implicit and explicit perceptual and semantic memory (Buckner and Koutstaal 1998), but also to test the properties of smaller populations of neurons in object-responsive areas of the human brain. For example, changes in the blood oxygenation level–dependent (BOLD) response following the repeated presentation of stimuli have been successfully utilized to probe differences in processing between fMRI response selections, action planning, and execution, showed only grasp-selective adaptation. These results suggest that, even in real action guidance, parietofrontal areas demonstrate differential involvement in visuomotor processing dependent on whether the action or the object has been previously experienced.

Because the phenomenon of repetition suppression or fMRI adaptation allows inferences about neural populations at a finer scale than the true spatial resolution, it is sometimes said to provide “hyper-resolution.” That is, as argued by Grill-Spector et al. (1999), within the confines of a functional area or even a smaller cluster of voxels, conventional subtraction methods may fail to distinguish between neurons with different selectivities. However, if these neurons show response change (e.g., suppression of activation) following back-to-back presentations of the same stimulus, the average activity within a cluster will differ, giving clues as to what stimulus properties are encoded within the area. In other words, the manipulation of experience with different stimuli and their features in the fMRI scanner have helped researchers understand what kind of visual and conceptual information is represented in the brain, where it is stored, and how this information might be processed within a larger cortical network (Grill-Spector et al. 2006).

To date, the majority of studies of the functional properties of different occipital (Grill-Spector et al. 1999), temporal (Huk et al. 2001; Stern et al. 1996), frontal (Wagner et al. 1997), or parietal areas (Hamilton and Grafton 2006, 2008; Shmuelof and Zohary 2005) have used repeated presentation of two-dimensional pictures of objects, visually presented words, visual motion displays, or action video clips. Although these stimuli have proved to be extremely effective in examining object- and movement-responsive areas in the cortex, probing the properties of the visuomotor-control circuit with pictures (James et al. 2002a; Rice et al. 2007; Valyear et al. 2006) and videos (Hamilton and Grafton 2006, 2008; Shmuelof and Zohary 2005), or even with a very limited number of hand gestures while playing with the videotaped opponent (Dinstein et al. 2007), rather than executing real, object-directed actions, restricts the conclusions that can be drawn. Of course, given the difficulties of studying real actions in the scanner (Culham et al. 2006), such an approach is quite valuable as a first pass to understanding visuomotor representations in the brain. However, simple viewing of action videos, responding to videotaped gestures, or even encoding action outcomes (Hamilton and Grafton 2008) may not tap the same neuronal mechanisms that are involved in the control of real object-directed actions (Goodale 2005), just like simulated actions do not tap neural circuits identical to those invoked by real actions (Króliczak et al. 2007).

Although there is certainly much evidence that actions can be affected by past experience, there is some question as to whether this can happen on short timescales (such as for two sequential trials). Behavioral studies in neurologically intact participants have found an absence of priming, according to two studies by Goodale and colleagues (Cant et al. 2005; Garofeanu et al. 2004). That is, they found no benefits in reaction time for a grasping action that was repeated on an object that had been grasped mere seconds (Cant et al. 2005) or

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minutes (Garofeanu et al. 2004) before, relative to a different grasp on a different object or a novel grasp on a novel object, respectively. Goodale and colleagues used these data as evidence to support their theory that, because objects and bodily positions are continually changing in the real world, visually guided actions such as grasping are computed de novo at the time of performance, rather than being stored over the longer term, as with visual perception (Goodale and Milner 1992). Although others have found some evidence of action priming (Craighero et al. 1996), Cant et al. (2005) suggested that these results may have arisen from the cognitive nature of the tasks used. Additional support for this theory comes from neuropsychology (Goodale et al. 1991, 1994; James et al. 2003), other behavioral experiments (as reviewed in Goodale et al. 2004, 2006), and neuroimaging studies (Króliczak et al. 2007; Singhal et al. 2005). In short, the finding that repeated actions do not lead to improved behavioral performance has been used to suggest that the action system may be largely impervious to recent actions. If so, the prediction would be that brain areas involved in these action tasks—that is, grasping—should be unaffected by prior trials.

Alternatively, there are numerous reasons to doubt this suggestion. All actions involve motor programs that have been built up during extensive long-term experience. However, practice effects—that is, effects that generalize to nontrained stimuli—are different from priming, which is specific to the trained stimuli (e.g., Garofeanu et al. 2004). Many action-related phenomena have been shown, both behaviorally and neurally, to depend on recent experience. For example, one of the most powerful of such effects is prism adaptation, whereby distortions in the mapping between vision and action lead to rapid and robust changes in behavior (e.g., Redding and Wallace 2006) and neural activation (Clower et al. 1996). Similarly, motor learning is well established and has been shown in areas such as primary motor cortex, the cerebellum, the parietal cortex, as well as in prefrontal areas (Halsband and Lange 2006). Typical examples of motor learning, though, are cases where sources of error are initially introduced and the sensorimotor system must recalibrate. They certainly suggest that learning is possible in areas that code actions, but do not address the question of whether quite recent, veridical and accurate experience can also change neural responses. Other behavioral experiments suggest that even the availability of haptic (Bingham et al. 2007) or visual feedback (Jakobson and Goodale 1991) may affect performance on subsequent trials. However, to our knowledge, none of the research to date has carefully characterized the brain areas that are affected by recent, veridical motor experience.

Here, our primary goal was to investigate whether fMRI adaptation would be observed within the parietal visuomotor circuits following the repetition of real object-directed actions. Our analyses focused on a human parietal area that is involved in visually guided grasping, the human anterior intraparietal sulcus (aIPS) area. Prior neurophysiological evidence from the putative functional equivalent of aIPS in the macaque (AIP) has suggested that hand-manipulation neurons encode both the object shape and the grip used during grasping (Murata et al. 2000). If the activity of similar neurons in human aIPS is modulated by recent trials, we would predict reduced fMRI responses in this area when the grip is repeated and when the object shape is repeated, relative to trials in which both of these attributes are different. If, however, as suggested by the absence of behavioral priming for grasping, these areas compute grasping plans de novo without influence from recent trials, then no repetition suppression should be observed. Regardless of the outcome in aIPS, we hypothesized that adaptation may still be seen outside the posterior parietal cortex (PPC), for example in premotor cortex, which has long been known to be involved in processing and maintaining information for movement selection until responses are executed (Passingham 1993). It was particularly important to us to test real actions rather than to rely on action imitation and observation associated with the mirror neuron system (e.g., Rizzolatti and Craighero 2004) because the processing in the latter may very well follow different principles and have much closer ties with memory systems.

**METHODS**

**Participants**

Four males and six females, ranging in age from 19 to 34 yr (mean age = 26.5, SD = 4.6 yr), participated in this experiment and were compensated financially for their time. All participants were right-handed and had normal or corrected-to-normal visual acuity. Prior to the study, they gave their informed consent. The experiment was approved by the Health Sciences Research Ethics Board at the University of Western Ontario and thus was carried out in accordance with the principles of the Helsinki 1964 Declaration.

**Apparatus, stimuli, and viewing conditions**

We developed a newer version of the stimulus presentation device, the grasping apparatus or “Grasparatus”, used in prior fMRI experiments in our lab (Culham et al. 2003; Króliczak et al. 2007). Like the Grasparatus, the newer “Grasparatus II” (custom designed and built at the University of Western Ontario Machine Services shop) is an MR-compatible octagonal drum for which the rotation is controlled pneumatically. However, in addition to a more reliable rotation mechanism, the Grasparatus II is more lightweight and durable, provides more degrees of freedom for positioning, and uses a Velcro-covered surface to present a wider variety of stimulus sequences (see Fig. 1A). Rotation of the drum is accomplished with four computer-controlled valves allowing brief (400 ms) air puffs to be sent from an air compressor via four tubes to a pneumatically driven piston and bolt, positioned on the inside of the drum that has eight grooves, each corresponding to one of the eight sides. By an appropriate sequence of air bursts, the piston can be pulled inward until it clicks into a new groove; the piston can then be pushed out to turn the drum, the bolt can be pushed into a hole to lock the drum while grasping occurs, and finally the bolt can be withdrawn to enable rotation of the drum for the next trial.

The use of a Velcro-covered drum surface on the Grasparatus II enabled the presentation of well-controlled sequences of stimuli. Because the drum is covered with the “loop” layer (fuzzier side) of the Velcro fastener, a series of eight objects was mounted on Velcro strips with the “hook” layer facing toward the drum. Four sets of eight objects were placed on Velcro strips, enabling the experimenter to quickly change all eight stimuli between runs. The 32 objects with different shapes, examples of which are shown in Fig. 1B, were made from white translucent plastic (and manufactured at the University’s Machine Services shop). The objects had a constant depth (0.6 cm), but varied in length (from 1.8 to 3.6 cm) and width (from 1.6 to 2.6 cm). One object of variable size, chosen pseudorandomly from a pair of objects similar across one dimension (such as the shape and extent of their length and/or width), was put on each of the eight faces of the drum, just in the center (see Fig. 1A, right).
Object orientations (either vertical or oblique) were selected to be comfortable for grasping with a precision grip on both the long and short axes. The sequences of object shapes and orientations were carefully selected such that after drum rotation, or its absence, one of five different testing conditions would be fulfilled (shown in Fig. 1C): 1) the same object was presented and the subject was given a prior auditory cue to grasp it the same way both times; 2) the same object was presented and the subject was cued to use a different grasp orientation; 3) a different object was presented but its shape along one of its dimensions enabled the same grasp; 4) a completely different object was presented at a different orientation, thus enabling only different kinds of grasps; or 5) a different object was presented for two repeated reaches. When exactly the same object was presented repeatedly, the drum was actually not rotated. (However, air puffs were still delivered to withdraw and push the bolt back in position, thus producing some noise and similar vibrations of the grasparatus.)

As in our previous study (Królczak et al. 2007), subjects and equipment were positioned to enable direct viewing of the objects (without a mirror) and grasping actions that were as natural and comfortable as possible given the constraints of the fMRI environment. The participant laid supine with the torso and head tilted at an angle of around 30° to see the objects on the grasparatus, which was placed about 10 cm above the subject’s pelvis. Given that testing took place in complete darkness, the presented object was made visible with a brief (300-ms) illumination of a superbright white light-emitting diode (LED) attached to the magnet-bore ceiling just above the coil and participant’s head. Throughout the experiment, participants were asked to fixate a small LED (0.2° of visual angle, fixed in a transparent plastic tube) attached to the ceiling of the magnet bore and positioned just over the center of the grasparatus (~10° of visual angle above). The position of the fixation light placed the stimuli in the participant’s lower visual field, quite a typical situation in everyday interactions with objects. More important, it prevented the eye strain that would occur with continuous gazing downward in the direction of the presented objects.

Head motion that would normally be caused by the reach-to-grasp movement was minimized by restraining the participant’s right upper arm in a hemicylindrical arm brace with Velcro straps. Although the arm brace immobilized the shoulder, it allowed a limited motion at the elbow for movements of the hand from the starting position around the navel toward the stimuli. The motion of the wrist was not limited at all and, as a result, the objects could be reached toward and/or grasped quite comfortably.

All the hardware (e.g., the valves controlling the air flow to the pneumatic piston rotating the drum of the grasparatus, LEDs) and the software (SuperLab Pro 3.0) were controlled by a Dell laptop computer that, at the beginning of each trial, received a trigger from the workstation controlling the acquisition of the functional data by the MRI scanner.

**Timing and instructions**

A slow event-related design, with trials spaced every 18 s, was used to allow the hemodynamic signal to return to baseline during the intertrial interval (ITI) and to prevent contamination of the BOLD response by any potential artifacts generated by the hand movement. A given trial consisted of a brief illumination of the presented object for 300 ms, followed by a 3-s-delay interval during which the first grasping movement (with the index finger and thumb) or reaching movement (to touch the object with knuckles only) took place. Subsequently, another 300-ms brief illumination of the same or different object took place, followed immediately by the second grasping or reaching movement and a rest period, both during a long ITI of 14.4 s. Prior to each back-to-back stimulus presentation (3.2 s

FIG. 1. The apparatus, stimuli, and the different conditions used in the study. A: the Grasparatus II—a new version of a pneumatically controlled apparatus for presenting 3-dimensional (3D) stimuli for grasping inside the functional magnetic resonance imaging (fMRI) scanner—is shown from 3 different perspectives, including the participant’s point of view (rightmost). The octagonal drum covered with Velcro enables presentation of a much wider variety of stimulus sequences. B: examples of 3D planar shapes used in the study. C: the 5 different conditions used: the same object was grasped in the same or a different way, different objects were grasped in the same or different ways, and different objects were also reached toward in different ways. Except for the brief illumination of the object (300 ms), back-to-back trials separated by 3 s were performed in complete darkness.

before), two auditory cues (each lasting 1 s) indicated which of the tasks a participant was about to perform in two of the upcoming back-to-back hand movements (compare with Fig. 1C).

When the auditory cues were “Grasp Long, Grasp Long” (or “Grasp Short, Grasp Short”), the participant was to get ready for grasping the first of the presented objects along its long (or, in the second case, short) axis, and then grasping the second of the objects along the same axis of elongation. If the grasparatus was not rotated before the second object presentation, this would result in a testing condition called “Same object Same grasp” (SoSg). If, however, the grasparatus was rotated but the relevant dimension of the subsequent object—i.e., its shape at the expected grasp points, but not necessarily its orientation—stayed the same, this would result in a “Different object Same grasp” (DoSg) condition. When the cues were “Grasp Long, Grasp Short” or vice versa, the participant was to get ready for grasping the first object along the axis indicated by the first cue and then changing the grasp respectively on the second presentation of the object. This time, if the grasparatus was not rotated before the second presentation of the object, it would result in a condition labeled “Same object Different grasp” (SoDg). If, however, the grasparatus was rotated and a completely different object—with a different or same orientation—was shown, the resulting condition was called “Different object Different grasp” (DoDg). Finally, when the cues were “Reach out, Reach out,” the participant’s task was to get ready for two consecutive reaching movements performed in the context of two different objects and the resulting condition was referred to as “Different object Reach Reach” (DoRR).

Notably, during precision grasping, participants were instructed not to lift the objects and thus movement durations were comparable for grasping and reaching trials (Cavina-Pratesi et al. 2007).

In the functional runs, each of the tasks (four possible back-to-back grasp types and the repeated reaching movement) was performed four times in a pseudorandom order constrained such that these trial types were fairly evenly distributed through the run (with each condition having an equal likelihood of being preceded by others). Each participant was typically tested with on average eight runs (minimum of six). Four different orders of trials within runs—each order with a completely different set of objects—were established before the study and participants received each run order at least once in a random sequence. Given that all subjects completed at least six runs, some of the orders were repeated at least once.

### Imaging parameters

We used a 4-Tesla whole-body MRI scanner (Varian, Palo Alto, CA; Siemens, Erlangen, Germany) at the Robarts Research Institute (London, ON, Canada). In all functional runs and an additional high-resolution anatomical scan, a transmit-receive, cylindrical birdcage radiofrequency head coil was utilized. The BOLD-sensitive signal (Ogawa et al. 1992) was used for functional volumes, collected using an optimized, T2*-weighted, segmented gradient echo echoplanar imaging (19.2 cm field of view, with 64 × 64 matrix size for an in-plane resolution of 3 mm, repetition time [TR] = 1 s, with two segments/plane for a volume acquisition time of 2 s; time to echo [TE] = 15 ms, flip angle [FA] = 45°, navigator-corrected). Depending on the size of the participant’s head, each functional volume consisted of ≥16 contiguous slices of 6-mm thickness (to cover approximately the same brain areas in each participant). The slice angle was about 30° from axial to sample occipital, parietal, posterior temporal, and posterior/superior frontal cortices. No gap was left between the slices and their acquisition order was noninterleaved. A T1-weighted anatomical reference volume was acquired along the same orientation as the functional images using a three-dimensional (3D) acquisition sequence (256 × 256 × 64 matrix size, in-plane resolution of 0.75 mm, 3.0-mm slice thickness, inversion time [TI] = 600 ms, TR = 11.5 ms, TE = 5.2 ms, FA = 11°).

### Data preprocessing

Brain Voyager QX (BV QX, version 1.8; Brain Innovation, Maastricht, The Netherlands) was used to analyze the data. Preprocessing involved numerous steps. First, data quality assurance was performed by watching cine-loop animation of each functional run to ensure there were no detectable artifacts or abrupt motions. Second, motion correction was applied using the standard BV QX motion-correction algorithm to align each functional volume to the one that was closest in time to the anatomical scan. The output showed no evidence of large, abrupt head motions (which often cannot be well corrected by such algorithms), although there were some volumes in which artifacts related to arm movement were visible (see following text). Third, linear trend removal and temporal high-pass filtering (to remove frequencies <3 cycles per run) were performed. (Given that we used multishot imaging to improve the signal/noise ratio, slice scan time correction was not possible.) Fourth, the first three volumes of each trial, which were sometimes contaminated by artifacts related to the arm movement (Birn et al. 1999; Culham 2006), were removed using Matlab v 6.1 (The MathWorks, Natick, MA) and the predictor functions were adjusted accordingly. We chose to remove contaminated volumes rather than to add predictors of no interest because there can be considerable variability in the magnitude of artifacts from trial to trial; thus predictors of no interest may remove the average effect of the artifacts, but the noise related to artifact variability could still reduce statistical power. Comparisons of these two approaches on sample data from our lab have found negligible differences in their ability to clean up data with artifacts.

The functional data were superimposed on anatomical brain images transformed into Talairach space (Talairach and Tournoux 1988). Spatial smoothing using a Gaussian kernel with full-width at half-maximum = 8 mm was used only before the third level—between-subjects analysis—i.e., prior to random-effects analyses across participants. We did not perform spatial smoothing at the first and second levels of analyses (i.e., for individual runs and across runs for a given participant) because aIPS is adjacent to somatosensory areas and smoothing typically obscures this distinction in individual subjects.

### General linear model

Statistical contrasts were performed using contrasts in the general linear model (GLM), which included the predictors, one for each condition: SoSg, SoDg, DoSg, DoDg, and DoRR. Each predictor was derived from a rectangular wave function (peak = 2-s duration) convolved with a standard hemodynamic response function (Brain Voyager QX’s default double-gamma hemodynamic response function [HRF]), shifted in time to account for the cutting of the first three artifact-susceptible volumes at the start of each trial. Notably, the HRF fit was validated by comparisons with the event-related responses averaged across all testing conditions to avoid preferential modeling of any one condition. Prior to analysis, the data were z-normalized; thus beta weights extracted from the active clusters represent an estimate of the magnitude of activation for each condition (constrained by the shape of the expected HRF) in units of z-scores.

### Region of interest approach

We used both a region of interest (ROI) approach and a voxelwise approach. The aim of the ROI approach was to directly test whether the dorsal-stream area aIPS would show grasp-related adaptation for repeated precision grasps and/or repeated objects. Given that aIPS is reliably positioned with respect to sulcal landmarks, even though those landmarks vary from individual to individual in Talairach space, the ROI method is the best way to identify aIPS without contamination from adjacent areas, particularly somatosensory and motor cortex. The aim of the voxelwise...
approach was to investigate what other brain areas become adapted during repeated back-to-back grasping trials and/or objects.

For ROI analysis, aIPS was identified by a balanced contrast of all grasping tasks with the reaching task: +SoSg + SoDg + DoSg + DoDg −4DoRR; compare with prior studies (Binkofski et al. 1998; Culham et al. 2003; Frey et al. 2005; Królczak et al. 2007). Even if, as some contend, grasping and reaching are not computationally distinct (e.g., Smeets and Brenner 2001) this subtraction can be considered a parametric contrast that serves well to isolate aIPS. The resulting clusters were defined in each individual using a threshold no more liberal than $P < 0.001$, uncorrected. Subsequently, from each ROI at the single subject level (i.e., left and right aIPS in each individual) we extracted the beta weights. We used SPSS v 15.0 statistical software (SPSS, Chicago, IL) to perform independent $2 \times 2$ repeated-measures ANOVAs to identify main effects for grasp (different vs. same) and object (different vs. same) and their possible interaction. Because aIPS was defined by a contrast of grasping versus reaching, there was no need to test whether all grasping conditions were associated with higher activation than baseline. (A personal one-sample t-tests confirmed that the activation for each condition was greater than the average activation during the intertrial baseline.)

**Voxelwise analyses of group activation using a random-effects model**

To determine what other brain areas may show activation changes during repeated grasping movements and repeated objects presentation, we performed a voxelwise random effects (RFX) analysis using a GLM across all ten participants. Statistical activation maps for the voxelwise analysis were set to $t(9) > 3.6$, uncorrected $P < 0.006$. We used the BV QX cluster threshold estimator, which takes input regarding the functional voxel size (3 mm$^3$ for 3D BV QX data), the estimated smoothness of a map and performs Monte Carlo simulations (1,000 iterations) to estimate the probability of clusters of a given size arising purely from chance. Because the minimum cluster size for a corrected $P$ value (0.05) is estimated separately for each map, the cluster sizes can differ for different comparisons (as detailed in Table 1).

Three voxelwise contrasts were performed: (1) to identify areas more activated by the average of the four grasping conditions than the reaching condition (+SoSg + SoDg + DoSg + DoDg −4DoRR contrast used earlier for localizing aIPS in individual subjects); 2) to identify areas showing a main effect of changing the grasp (−SoSg + SoDg − DoSg + DoDg); and 3) to identify areas showing a main effect of changing the object (−SoSg − SoDg + DoSg + DoDg).

On identification of significant activation clusters, the overall pattern of effects within each cluster was characterized by performing a series of GLM contrasts (using the ROI-GLM function of Brain Voyager) on the beta weights extracted from all significantly activated voxels within a (1 cm)$^3$ cluster either centered around the average coordinates of a given area of interest, e.g., average aIPS coordinates (cf. Frey et al. 2005), or a distinct activation peak. Specifically, we performed main effect contrasts, using predictors for different grasp versus same grasp and different object versus same object. We also tested whether the grasp and object effects interacted. In cases where significant interactions were observed, they were further investigated by $t$-test for the six possible comparisons between two conditions.

The anatomical location of the active clusters was validated in two ways: by manual comparison with an atlas (Damasio 1995) and by overlaying activation maps on the population-average, landmark- and surface-based (PALS) atlas of Van Essen (2005) using CARET 5.5 Brain Mapping Software (Van Essen et al. 2001). To this end, volumetric group average data from BV QX were converted to NIFTI files and rethresholded. Subsequently, two mapping techniques were utilized: 1) average-fiducial mapping (AFM) was used to create surface renderings by a simple projection of the standard space group average data onto the PALS atlas; 2) multifiducial mapping (MFM) was used to validate the robustness of the effects we observed by projecting these same average data onto a set of 12 individual brains, then reaveraging them to account for individual variations in cortical topography (Van Essen 2005). Because the MFM were showing virtually the same patterns of activation, we decided to stick with the standard AFM procedure.

**RESULTS**

**ROI analysis**

**LOCALIZATION OF THE ANTERIOR INTRAPARIETAL SULCUS (AIPS).** Using a balanced contrast of all grasping conditions (irrespective of the back-to-back grasp type and/or presented object) versus a reaching task, we first identified area aIPS. As shown in Fig. 2, this was done by selecting an activation cluster located at or near the junction of the intraparietal sulcus (IPS) and the inferior segment of the postcentral sulcus (PCS). We were able to identify aIPS bilaterally in all ten participants and there was typically one focus of activation around the junction of IPS and PCS in each hemisphere.

The average Talairach coordinates of aIPS were in very good agreement with aIPS coordinates from previous fMRI experiments (Binkofski et al. 1998; Culham et al. 2003; Frey et al. 2005; Królczak et al. 2007). The beta weights that were subsequently obtained for each individual from the active voxels identified as left and right aIPS and the average betas are illustrated in Fig. 2, A and B.

**ADAPTATION IN LEFT AIPS.** We found that left aIPS showed the largest decrease in activation (i.e., the greatest fMRI adaptation) when the same grasping movements were repeated compared with different grasping movements, irrespective of the objects involved. There was also a decrease in activation following repeated presentation of the same object compared with the presentation of different objects, irrespective of the grasp used. In particular, a 2 (grasp type) × 2 (object type) repeated-measures ANOVA revealed that there was a significant main effect of grasp [same vs. different; $F(1, 9) = 78, P < 0.001$], indicating that repeated performance of the same grasping movements was associated with significantly lower activation than different grasping movements, no matter what objects (same or different) they were directed at. There was also a significant main effect of object [$F(1, 9) = 15.1, P < 0.01$], such that repeated presentation of the same objects was associated with significantly lower activation than successive presentation of different objects (no matter what type of grasping was involved). There was a trend toward significance for the grasp by object interaction [$F(1, 9) = 3.9, P = 0.08$], such that object adaptation tended to be stronger when the grasp remained the same than when the grasp changed (i.e., $DoSg - SoSg > DoDg - SoDg$).

**ADAPTATION IN RIGHT AIPS.** Similarly to left aIPS, we found that right aIPS also showed the largest adaptation when the same grasping movements were repeated (vs. different grasping movements), irrespective of the presented objects. There was also adaptation following repeated presentation of the same object (vs. different objects), irrespective of the grasp used. In particular, a 2 × 2 repeated-measures ANOVA revealed that the main effect of grasp was significant [$F(1, 9) = 34.9, P < 0.001$]. That is, in right aIPS, repeated grasping movements were also associated with significantly lower activation than different grasping movements, no matter what objects were presented. The main effect of object...
based on patterns observed in all voxels significantly active within (1 cm)³ centered on average coordinates or activation peak—expressed as volume size in mm³ GRASP NETWORK. As shown in Fig. 3 in right aIPS was also significant • VOL 100 • NOVEMBER 2008 • www.jn.org

TABLE 1. Average or peak coordinates, cluster size, and effects observed in the anterior intraparietal sulcus, regions identified with a localizer contrast, and regions showing adaptation due to grasp and object repetition

<table>
<thead>
<tr>
<th>Region</th>
<th>Talairach Coordinates</th>
<th>Volume, mm³</th>
<th>Grasping &gt; Reaching</th>
<th>Main Effect of Grasp</th>
<th>Main Effect of Object</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Average location of anterior intraparietal sulcus (aIPS) as identified in individual subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left anterior intraparietal sulcus (aIPS)</td>
<td>−44 −34 42</td>
<td>990</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.6</td>
</tr>
<tr>
<td>Right anterior intraparietal sulcus (aIPS)</td>
<td>46 −34 44</td>
<td>995</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.4</td>
</tr>
<tr>
<td><strong>B. Localizer (Grasping &gt; Reaching): t(9) = 3.6, P &lt; 0.006, cluster threshold 459 mm³</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left anterior intraparietal sulcus (aIPS)</td>
<td>−39 −46 39</td>
<td>968</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>1.0</td>
</tr>
<tr>
<td>Right anterior intraparietal sulcus (aIPS)</td>
<td>42 −40 48</td>
<td>1,000</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>*</td>
</tr>
<tr>
<td>Left mid superior parietal lobe (mid-SPL)</td>
<td>−24 −65 37</td>
<td>771</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>0.5</td>
</tr>
<tr>
<td>Right mid superior parietal lobe (mid-SPL)</td>
<td>22 −58 40</td>
<td>772</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>0.4</td>
</tr>
<tr>
<td>Left inferior postcentral sulcus (iPCS)</td>
<td>−56 −19 31</td>
<td>641</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.7</td>
</tr>
<tr>
<td>Right inferior postcentral sulcus (iPCS)</td>
<td>60 −19 33</td>
<td>990</td>
<td>***</td>
<td>***</td>
<td>0.2</td>
<td>0.9</td>
</tr>
<tr>
<td>Left dorsal premotor cortex (PMd)</td>
<td>−27 −16 55</td>
<td>905</td>
<td>***</td>
<td>***</td>
<td>0.1</td>
<td>0.6</td>
</tr>
<tr>
<td>Right dorsal premotor cortex (PMd)</td>
<td>25 −10 49</td>
<td>901</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>0.9</td>
</tr>
<tr>
<td>Right presupplementary motor area (pre-SMA)</td>
<td>3 19 48</td>
<td>783</td>
<td>***</td>
<td>***</td>
<td>0.06</td>
<td>**</td>
</tr>
<tr>
<td>Right ventral premotor cortex (PMv)</td>
<td>51 3 28</td>
<td>756</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.3</td>
</tr>
<tr>
<td>Right caudal inferior temporal gyrus (cITG)</td>
<td>53 −50 −16</td>
<td>364</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.3</td>
</tr>
<tr>
<td>Left cerebellum</td>
<td>−24 −49 −28</td>
<td>555</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.4</td>
</tr>
<tr>
<td>Right cerebellum</td>
<td>21 −46 −24</td>
<td>930</td>
<td>0.4</td>
<td>0.9</td>
<td>0.0</td>
<td>*</td>
</tr>
<tr>
<td><strong>C. Grasp adaptation (Different Grasp &gt; Same Grasp): t(9) = 3.6, P &lt; 0.006, cluster threshold 282 mm³</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Left anterior intraparietal sulcus (aIPS)</td>
<td>−47 −40 46</td>
<td>805</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.2</td>
</tr>
<tr>
<td>Right anterior intraparietal sulcus (aIPS)</td>
<td>33 −49 43</td>
<td>591</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>0.4</td>
</tr>
<tr>
<td>Left mid superior parietal lobe (mid-SPL)</td>
<td>−33 −44 35</td>
<td>678</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.8</td>
</tr>
<tr>
<td>Right mid superior parietal lobe (mid-SPL)</td>
<td>29 −55 41</td>
<td>375</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>0.2</td>
</tr>
<tr>
<td>Left inferior postcentral sulcus (iPCS)</td>
<td>−48 −26 37</td>
<td>599</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>Right inferior postcentral sulcus (iPCS)</td>
<td>59 −23 37</td>
<td>528</td>
<td>***</td>
<td>***</td>
<td>0.07</td>
<td>1.0</td>
</tr>
<tr>
<td>Left primary motor cortex (MI)</td>
<td>−33 −10 40</td>
<td>378</td>
<td>***</td>
<td>***</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Left dorsal premotor cortex (PMd)</td>
<td>−25 −10 52</td>
<td>481</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>0.8</td>
</tr>
<tr>
<td>Right dorsal premotor cortex (PMd)</td>
<td>25 −13 58</td>
<td>536</td>
<td>***</td>
<td>***</td>
<td>0.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Left caudal superior frontal gyrus (cSFG)</td>
<td>−21 −2 55</td>
<td>597</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>0.3</td>
</tr>
<tr>
<td>Right caudal superior frontal gyrus (cSFG)</td>
<td>18 −13 66</td>
<td>675</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>0.8</td>
</tr>
<tr>
<td>Left ventral premotor cortex (PMv)</td>
<td>47 3 31</td>
<td>358</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>0.5</td>
</tr>
<tr>
<td>Left middle frontal gyrus (MFG)</td>
<td>−41 24 34</td>
<td>522</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>0.4</td>
</tr>
<tr>
<td>Left midbrain</td>
<td>−9 −11 −7</td>
<td>463</td>
<td>***</td>
<td>***</td>
<td>0.2</td>
<td>*</td>
</tr>
<tr>
<td><strong>D. Object adaptation (Different Object &gt; Same Object): t(9) = 3.6, P &lt; 0.006, cluster threshold 291 mm³</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left anterior intraparietal sulcus (aIPS)</td>
<td>−42 −43 39</td>
<td>751</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.5</td>
</tr>
<tr>
<td>Right anterior intraparietal sulcus (aIPS)</td>
<td>48 −34 45</td>
<td>658</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.5</td>
</tr>
<tr>
<td>Left mid superior parietal lobe (mid-SPL)</td>
<td>37 −56 34</td>
<td>425</td>
<td>***</td>
<td>***</td>
<td>**</td>
<td>0.8</td>
</tr>
<tr>
<td>Left supramarginal gyrus (SMG)</td>
<td>−51 −39 45</td>
<td>510</td>
<td>***</td>
<td>***</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Right caudal superior frontal gyrus (cSFG)</td>
<td>−18 12 47</td>
<td>309</td>
<td>***</td>
<td>0.4</td>
<td>**</td>
<td>0.5</td>
</tr>
<tr>
<td>Right ventral premotor cortex (PMv)</td>
<td>43 6 29</td>
<td>458</td>
<td>***</td>
<td>0.1</td>
<td>***</td>
<td>*</td>
</tr>
<tr>
<td>Left occipito-temporal sulcus/posterior fusiform gyrus (OTS/Pfus)</td>
<td>−48 −52 −15</td>
<td>571</td>
<td>***</td>
<td>0.2</td>
<td>***</td>
<td>0.06</td>
</tr>
<tr>
<td>Right occipito-temporal sulcus/posterior fusiform gyrus (OTS/Pfus)</td>
<td>50 −48 18</td>
<td>447</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>**</td>
</tr>
</tbody>
</table>

For each region identified with a given contrast at t = 3.6, P < 0.006 in the random-effects analysis, statistical significance (P values) for ROI GLM contrasts based on patterns observed in all voxels significantly active within (1 cm)³ centered on average coordinates or activation peak—expressed as volume size in mm³ and in Talairach coordinates, respectively—are reported.

in right aIPS was also significant [F(1,9) = 9.1, P < 0.05]. That is, as in left aIPS, repeated presentation of the same objects was associated with significantly lower activation than successive presentation of different objects (irrespective of the grasp type involved). The grasp by object interaction, however, was not significant [F(1,9) = 3.1, P = 0.1].

Voxelwise analysis

The full results of the voxelwise analyses are presented in Table 1 with Fig. 3, A–C showing specific clusters.

GRASP NETWORK. As shown in Fig. 3A, a contrast of grasping versus reaching revealed significant bilateral clusters of activation within and along the rostral and caudal banks of the intraparietal sulcus (IPS). This activation included area aIPS, bilaterally. In the right hemisphere, the activation extends more onto the lateral convexity of the supramarginal gyrus (SMG) in the inferior parietal lobe (IPL) and further into inferior postcentral sulcus (iPCS), whereas in the left hemisphere it extends more to the anterior parts of the superior parietal gyrus (SPG) of the superior parietal lobe (SPL) and to the neighboring somatosensory cortex. A distinct focus of activation was also observed in SPL, bilaterally, midway along its anterior–posterior extent (mid-SPL). We also observed pronounced bilateral activity at the junction of the superior frontal sulcus (SFS) and precentral sulcus, which we will refer to as dorsal premotor
(PMd) cortex. This PMd activation extended onto the caudal superior frontal gyrus (cSFG) and, in the right hemisphere, into the motor cortex. The activation in the ventral premotor cortex (PMv) was only on the right, as was the activation in the presupplementary motor cortex (pre-SMA). Finally, we also saw a large cluster of activation in the right caudal inferior temporal gyrus (cITG) and this activity extended partially into the inferior temporal sulcus. In addition to the cortical activations shown on the surface renderings, the grasping versus reaching contrast identified two clusters of activation within the cerebellum.

Table 1 provides a list of activated areas, their coordinates, and the significance of the major contrasts. All of the areas reported earlier showed a main effect of grasp adaptation in post hoc contrasts, such that repeated grasping led to a significantly lower activation than different grasping. Except for the left PMd, right iPCS, and right cerebellum, all of these areas also showed a main effect of object adaptation, such that repeated presentation of an object led to a significantly lower activation than a presentation of a different object (with pre-SMA just missing significance level). Finally, except for right aIPS, pre-SMA, and cITG, none of the areas showed a significant interaction. In right aIPS, adaptation in the SoDg condition did not differ from DoDg and the two were significantly different both from the SoSg condition, which showed the best adaptation or a signal decrease, and the DoDg condition, in which the fMRI signal change was the highest (i.e., (SoSg < [SoDg = DoSg]) < DoDg)). In pre-SMA and cITG, there was an equal adaptation in the three conditions in which either the object or the grasp remained the same (i.e., SoSg, SoDg, and DoSg) and all were significantly different from DoDg (i.e., [SoSg = SoDg = DoSg] < DoDg). The right cerebellum showed neither of the two main effects of adaptation, but did show a significant interaction (such that adaptation was best in the DoSg condition, but differed significantly only from the DoDg condition).

**GRASP ADAPTATION NETWORK.** A similar, although somewhat smaller in its extent, pattern of parietal and dorsal premotor activation was observed when performance of different grasping movements was contrasted with the same grasping movements (as shown in Fig. 3B). The most important difference was now the absence of this effect in cITG and right PMv. Notably, there was now a small, but significant, cluster of activation in PMv on the left, as well as a large more anterior cluster in the left middle frontal gyrus (MFG). Grasp adaptation was also observed in the left central sulcus, likely in the hand area of the primary motor cortex (M1). In addition, subcortical activation was observed in the left midbrain.

Given the contrast used to localize these areas, all of them necessarily showed a main effect of grasp adaptation in the post hoc contrasts. Except for left M1, right PMd, the neighboring cSFG, and the left midbrain, all of these areas also showed a main effect of object, such that repeated presentation of an object led to a significantly lower activation than a presentation of a different object (with right iPCS just missing the significance cutoff). The left iPCS showed a significant interaction, such that object adaptation tended to be stronger when the grasp remained the same than when the grasp changed (i.e., DoSg > SoSg > DoDg > SoDg). The left midbrain also showed an interaction such that there was an equal adaptation in the three conditions in which either the object or the grasp remained the same (i.e., SoSg = SoDg = DoSg) < DoDg).

**OBJECT ADAPTATION NETWORK.** Areas that were adapted by repeated presentations of the objects were found in temporal and parietofrontal regions. Within the ventral stream, object adaptation was observed bilaterally and was located primarily in the occipitotemporal sulcus (OTS). While in the right hemisphere this activity extended more anteriorly and also superiorly (onto cITG), in both hemispheres it extended medially onto the posterior fusiform gyrus (pFus). This is why we
FIG. 3. Surface renderings and transverse slices representing activation in the three contrasts of the study. In A–C, the volumetric surface renderings in the top panels illustrate significant group average activations mapped onto the population-average, landmark- and surface-based (PALS) atlas in CARET using average-fiducial mapping. The transverse slices in the bottom panels display group mean activations projected onto a single participant’s high-resolution T1-weighted anatomical scan. The activation is displayed in neurological convention (i.e., right hemisphere in on the right) and is shown in hues corresponding to the color bar between the panels. A: the grasp network. A contrast of “+Grasping – Reaching” (grasping vs. reaching) revealed activation in the dorsal stream, and a single cluster of activation in the ventral stream. In particular, activation was observed bilaterally in the intraparietal sulcus (IPS), including its most anterior part (aIPS), the inferior postcentral sulcus (iPCS), the supramarginal gyrus (SMG) of the inferior parietal lobe (IPL), and the superior parietal gyrus (SPG) of the superior parietal lobe (SPL). From SPG, the activity extended to the left somatosensory cortex. The activity in mid-SPL was bilateral. There was also bilateral activation in the dorsal premotor cortex (PMd) and it extended to the primary motor cortex (M1) on the right; the ventral premotor (PMv) cortex was activated on the right, as was the presupplementary motor cortex (pre-SMA). Activation in the ventral stream was only in the right caudal inferior temporal gyrus (cITG). B: the grasp adaptation network. A contrast of “+Different grasp – Same grasp” demonstrates the effect of grasp repetition (i.e., grasp selectivity) such that repeated grasping results in a lower and nonrepeated grasping in higher activation in a given cluster. Significantly lower activation (i.e., adaptation) during repeated grasping was observed in the same parietal areas as in A, but was smaller in its extent. Moreover, activation in PMv was on the left and there was also activation in the middle frontal gyrus (MFG), left M1, and in the left midbrain. C: the object adaptation network. A contrast of “+Different object – Same object” demonstrates the effect of object repetition (i.e., object selectivity) such that repeated presentation of an object results in a lower and nonrepeated presentation in higher activation in a given cluster. Significant adaptation was observed bilaterally in IPS (including aIPS), left SMG, and right mid-SPL. PMv was activated on the right, the caudal superior frontal sulcus (cSFS) on the left, and the occipitotemporal sulcus/posterior fusiform gyrus (OTS/pFus) bilaterally. D: a direct comparison of grasp and object adaptation. The common network for the 2 effects was located entirely in the parietal cortex: bilateral IPS (including aIPS), left SMG, and right mid-SPL. E: anatomical landmarks. Most of the abbreviations have already been defined in A–C. LO, lateral occipital cortex; cSFG, caudal superior frontal gyrus.
will refer to these two ventral clusters as OTS/pFus. In addition, object adaptation was observed within IPS, extending to left SMG, in right mid-SPL, right PMv, and the caudal part of the left superior frontal sulcus (SFS). For details, see Fig. 3C.

In the post hoc contrasts, bilateral aIPS, right mid-SPL, left SMG, and right OTS/pFus (but not left SFS, right PMv, and left OTS/pFus) also showed a main effect of grasp. Three of the areas also showed a significant interaction. In left SMG, adaptation in the SoSg condition did not differ from that in DoSg and the two were significantly different both from SoSg, where adaptation was best, and DoDg, where the signal change was the highest (i.e., \{SoSg < [SoDg = DoSg]\} <DoDg). In right PMv, on the other hand, adaptation in SoSg and SoDg was equal and both were significantly different from DoSg, which also showed significant adaptation compared with DoDg (i.e., \{[SoSg = SoDg] <DoSg \} <DoDg). In right OTS/pFus (and also the left OTS/pFus where the interaction just missed the significance level), there was an equal adaptation in the three conditions in which either the object or the grasp remained the same (\{SoSg = SoDg = DoSg\} <DoDg).

**DISCUSSION**

Here we have shown that neural mechanisms for grasping in the human brain can be affected by the prior history of real actions. Such effects were observed in area aIPS and adjacent cortex, the superior parietal cortex, and premotor cortex. Specifically, these regions demonstrated reduced fMRI activation when either the grasp used or the target object was repeated, indicating that neurons within the parietofrontal network known to mediate the control of action compute both the grasp and the object. The results we found in human aIPS are consistent with the data showing that individual neurons in macaque AIP are tuned to both the grasp and the object (Murata et al. 2000; Sakata et al. 1995). This provides converging evidence for the case that human aIPS and macaque AIP are functionally similar and, possibly, homologous (Culham 2004). However, the more interesting aspect of these results is that they were observed using an fMRI adaptation design with real actions to real objects. This in turn suggests that the dorsal stream can indeed be influenced by past events.

These results are surprising given the proposal that, because the world and the actor’s body are typically in flux, it makes little sense to store motor programs and continually update them (Goodale and Milner 1992; Milner and Goodale 1995). Instead, it is thought to be more computationally efficient to simply generate the program at the time the action is required. Indeed studies consistent with this view are abundant (Goodale et al. 1994; Króliczak et al. 2006a,b; Westwood and Goodale 2003). However, our results here suggest that even in a system that does not explicitly store motor programs in the dorsal stream over the long term, visuomotor programming can be affected by repetition.

**Mechanisms for fMRI adaptation**

How might such influences of recent trials be implemented within parietofrontal cortex? Theories of fMRI adaptation suggest that such effects might occur through three possible mechanisms or some combination thereof (Grill-Spector et al. 2006). First, in the fatigue model, fMRI adaptation may occur because of reduced activation within a neural network for a repeated event. In this view, a decrease in responses to repeated grasps or objects may simply occur because neurons in the dorsal stream are less responsive the second time. Second, in the sharpening model (Wiggs and Martin 1998), fMRI adaptation may occur because neurons become more precisely tuned. Given that neurons in macaque AIP were previously shown to be selective for both object shape and for the grasp used (Murata et al. 2000; Sakata et al. 1995), a sharpening model would predict that with repeated presentations this tuning becomes more specific. As a result, the responses within neurons selective for a particular shape would remain high, but other neurons tuned to similar but not identical shapes or grasps would become less responsive, thus reducing the overall fMRI response. Third, in the facilitation model (James and Gauthier 2006), the cascade of neural events may occur more rapidly and, although the peak response may remain high, the reduced response duration could lead to a lower fMRI response. Recent data suggest that fMRI adaptation—and indeed all fMRI activation (Logothetis 2003)—may reflect synaptic inputs to an area rather than outputs (Sawamura et al. 2006; Tolias et al. 2005). Thus it may be that the areas that show grasp- and object-selective repetition suppression do so because of feedforward or feedback connections.

Regardless of which of these possible explanations for repetition suppression (or their combination) is most appropriate to account for the repetition suppression we observed, our results nevertheless indicate that action-related areas in the parietofrontal network are affected by recent events. The reduction in compensatory blood oxygenation that occurs with repeated stimuli suggests that the computation of a grasp in these areas requires less energy the second time around.

**Relationship between fMRI adaptation and behavioral priming**

Given our evidence here for effects on visuomotor brain areas with repeated grasps and objects, an obvious question is why this has not been reflected in studies of behavioral priming to date. That is, why are subjects unable to respond faster when performing repeated actions or actions on repeated objects? There are several possible explanations. If, as the fatigue model suggests, repeated actions simply lead to reduced activation both at the level of individual neurons and the fMRI population response, then processing may not necessarily be more efficient and thus behavioral priming may not be expected. Others have suggested that the fatigue model may be more appropriate for earlier sensory areas (Grill-Spector et al. 2006) and that the correlation between neural priming and behavioral priming is much stronger in prefrontal areas than in posterior areas such as extrastriate cortex (Schartel et al. 2007). However, if the sharpening or facilitation models are correct, then more accurate or faster grasps may be predicted.

Evidence of behavioral priming for motor tasks has been equivocal, with priming observed only in studies with a more cognitive nature. For example, one experiment found that a prime regarding a remembered orientation could facilitate reaction times (Craighero et al. 1996); however, this study has been criticized because the dependence on memory may recruit the ventral stream, for which priming is expected (Cant et al. 2005). In a different experiment, the effects of obstacles on
hand paths persisted across repeated trials (Jax and Rosenbaum 2007), but, again, the task of “controlling” a schematic model of the arm and the use of virtual targets and obstacles may have recruited cognitive mechanisms.

Only two studies (Cant et al. 2005; Garofeanu et al. 2004) have examined priming of actions using tasks with no obvious cognitive component (Goodale et al. 2006). In one experiment by Cant and colleagues (2005), participants showed no improvement in reaction time when presented with objects that had the same shape and/or orientation as in a previous trial, regardless of whether the first trial simply involved viewing the objects or executing a fully formed grasp. The grasp used, though, was a whole hand grasp—a power grip—rather than the more exacting precision grip with finger and thumb, for which aIPS may be specialized (Begliomini et al. 2007). In other words, an absence of priming for orientation during the power grip does not preclude the possibility of priming for intrinsic object features such as shape when precision grip and a larger set of objects are used. Interestingly, though, even with the use of a wider range of objects, such as common tools and utensils (typically requiring a whole hand grasp), similar results were found (Garofeanu et al. 2004), but in this case, the priming was tested over a longer term (several minutes). Our current study does not indicate whether fMRI adaptation effects in the dorsal stream can last longer than a few seconds. Moreover, past fMRI investigations have suggested that short-term adaptation and long-term neural priming can be dissociated (Ganel et al. 2006).

Intriguingly, some past kinematic studies have suggested that the learned properties of objects can influence grasp parameters over the long term. In a series of experiments, Haffenden and Goodale (2000, 2002a,b) found that when participants learned an association between object attributes and size (e.g., that yellow cubes were always larger than red cubes) then, similarly to perceptual judgments in the form of manual estimates, the association also affected the grasp (as measured by the maximum grip aperture). However, this was the case only if the cue reflected material properties of objects, such as color or texture (Haffenden and Goodale 2000, 2002a), and if the object shape (Haffenden and Goodale 2000) and location (Haffenden and Goodale 2002b) remained constant. Notably, although these behavioral results suggest that the grasp can be affected by the long-term history of past interactions, they do not address whether the changes reflect processing within the dorsal or ventral streams, or the cross talk between them. It would also be interesting to see whether the grasp- and object-selective adaptation effects we observed in aIPS and other areas would survive a change in object position.

Based on our fMRI results showing adaptation in a grasp-selective network, we suggest that behavioral priming effects should be revisited using a paradigm with a scope similar to that of our fMRI design. That is, priming of grasping could be investigated over short intervals (on the order of a few seconds or less) for a wide variety of objects and orientations, in a task that does not explicitly rely on memory or other cognitive mechanisms. Perhaps most important, given that both of the projects that found no evidence of behavioral priming used only reaction time as a dependent measure (Cant et al. 2005; Garofeanu et al. 2004), it would be ideal, as in more recent movement precueing paradigms (Królczak et al. 2006b), to measure other kinematic variables such as grip scaling over time, maximum grip aperture and the time at which it occurs, and movement times.

**Adaptation effects in parietal cortex**

Adaptation to both repeated grasps and repeated objects within aIPS is consistent with the grasp and object tuning observed in macaque AIP (Murata et al. 2000). These results are also consistent with the grasp and object selectivity found in human aIPS when subjects view an actor grasping objects (Shmuelof and Zohary 2005), but extend those findings to real actions. Other labs using fMRI adaptation, however, have suggested that aIPS codes not the detailed kinematics of an action, but rather the outcome (Hamilton and Grafton 2006, 2008). In this case, however, the stimuli were movies of observed actions and it is possible that the properties and tuning differ between observed and executed actions. Indeed, a recent fMRI adaptation study (Dinstein et al. 2007) found no cross-adaptation between observed and executed actions (though this is surprising given that “mirror neurons” in macaque cortex show similar preferences for observed and executed actions).

Although aIPS may be considered part of the dorsal stream, Rizzolatti and Matelli (2003) suggested the aIPS–PMv circuit forms a “ventro-dorsal” stream with different functionality than the V6A/medial intraparietal–PMd circuit, which forms a “dorso-dorsal” stream. In their view, the ventro-dorsal stream plays a greater role in action understanding and has closer ties with the ventral stream. Indeed, recent anatomical tracing studies in the macaque (Borra et al. 2008) have revealed direct connections from the inferotemporal cortex to AIP. However, the existence of such connections from ventral object-selective cortex to aIPS does not mean they are always in use. For example, neuropsychological data suggest that a patient with visual form agnosia can accurately grasp objects in real time (and shows aIPS activation) without input from a key object-selective area in the ventral stream, the lateral occipital (LO) area (James et al. 2003). It is only under more challenging circumstances, such as delayed grasping, that impairments in grasping are revealed (Goodale et al. 1994).

In addition to aIPS, we also observed grasp- and object-selective adaptation in mid-SPL. This focus may be consistent with the human parietal eye fields or an orientation-selective area that some have suggested to involve orientation coding (compare with the metanalysis and papers cited in Culham et al. 2006). Importantly, in the two conditions of our experiment where the object changed (DoSg and DoDg), the primary axis of orientation of the object would also change 50% of the time (given a preset object and orientation order and a single drum rotation to the next consecutive object). In contrast, in the two conditions in which the object identity remained the same (SoSg and SoDg) during the two back-to-back trials (given no drum rotation, but different instructional cue), obviously no orientation change occurred. Thus our current paradigm does not allow us to determine conclusively the degree to which object-selective adaptation—in mid-SPL and elsewhere—was driven by changes in object identity versus object orientation.
Adaptation effects in frontal cortex

Although we have emphasized the finding of grasp- and object-selective activation decrease within the posterior parietal cortex (including SPL and IPL), where we found some clear overlap of the two effects (cf. Fig. 3D), we also observed the two types of adaptation in three regions of the frontal lobe: 1) the ventral premotor cortex, with grasp adaptation present in left PMv, and object adaptation in right PMv; 2) the dorsal premotor cortex, with grasp adaptation observed bilaterally (and object adaptation found only in an adjacent cluster in left cSFS); and 3) the left middle frontal gyrus, where only grasp adaptation was found. Notably, within the left-lateralized network, all the frontal areas selective for grasp type (i.e., showing grasp adaptation), also showed object selectivity within their respective ROIs. However, neither of the two frontal areas showing object selectivity was also selective for grasp type. In other words, it seems that in the frontal lobe, particularly on the left, neural populations demonstrating grasp selectivity (e.g., within left PMv) would also show some degree of sensitivity to different object features (here shape), whereas populations showing object selectivity may not necessarily be sensitive to different kinds of grasp.

Although macaque neurophysiology suggests that PMv (area F5) has close anatomical and functional interconnections with aIPS (Borra et al. 2008; Luppino et al. 1999) and is also critical in the guidance of the grasping limb (Fogassi et al. 2001), human fMRI studies have had mixed success in obtaining PMv activation for grasping (Culham et al. 2003; Frey et al. 2005; Grezes and Decety 2003). Unlike our prior studies (Culham et al. 2003; Króliczak et al. 2007), here we did observe the involvement of area PMv. There might be two reasons for this: in the current experiment participants had to maintain in memory the cues that determined the visuomotor programming for the two consecutive grasping movements; moreover, we smoothed the data, making it more likely that the activation would survive intersubject averaging. A similar adaptation pattern, indicating robust grasp selectivity, was observed in left MFG, an area that has also been observed in human fMRI of motor imagery (Grezes and Decety 2002).

In contrast to aIPS (bilaterally) and left PMv, dorsal premotor areas showed less (left hemisphere) or no (right hemisphere) selectivity for object shape, although grasp selectivity was robust. A recent human transcranial magnetic stimulation (TMS) study (Davare et al. 2006) reported a similar dissociation between PMv and PMd. Specifically, TMS to PMv disrupted the positioning of the fingers on the object, whereas TMS to PMd disrupted the later lifting phase of the movement. Presumably the earlier grasping phase relies on object shape to a greater degree than the later lifting phase. Thus these results are consistent with our findings that object shape is more important in PMv than in PMd.

One caveat of our experiment is that our task involved semantic instructions regarding which axis of the object to grasp. This was necessary because it would have been very difficult to have subjects spontaneously choose the grasp posture themselves while ensuring enough trials with different grasps. It could be argued, though, that the effects we observed, for grasp adaptation in particular, resulted from the repetition of the instruction/rule rather than the grasp per se. We believe this is less of a concern for aIPS, which is not modulated by cognitive judgments (Cavina-Pratesi et al. 2007), but may be somewhat relevant for premotor cortex. However, even though the instructional cues direct participants’ attention to the axis of an object (and the resulting orientation) that should be identified before any movement can take place, it is not the case that the intrinsic features of the object do not drive the behavior at all. On the contrary, the object orientation and shape are as important as—if not much more important than—the prior instructional cues. Although it is true that instructions must be held in memory, they merely affect the “preparatory set.” In other words, motor programming and the immediate grasp execution—the two inseparable phases of a response that were explicitly modeled in our study and that most likely contribute to a much larger fMRI signal change than a cue—cannot take place until the target object becomes visible. Moreover, no learning of any kind (in particular, any abstract rules) is involved in our experiment (cf. Passingham et al. 2000). Finally, it should be emphasized that participants in our study did not have to make any high-level decisions, such as selecting between different categories of actions on the basis of abstract cues (cf. Passingham and Toni 2001), and there is a one-to-one correspondence between the instructional cue and the response. Thus we would argue that a simple repetition of a cue could not have been a major factor contributing to the robustness of our results.

Object adaptation effects in temporal cortex

We also observed object adaptation bilaterally in the ventral stream, where the activity in the occipitotemporal sulcus also extended onto the posterior fusiform gyrus. This OTS/pFus activation was not in the classic region of the lateral occipital area (LO, within the larger lateral occipital complex [LOC]; Grill-Spector et al. 2001), but rather more ventral and anterior. It was also somewhat ventral and anterior to the tactile–visual division of LOC (LOtv) described by Amedi and colleagues (2001, 2002). However, it did appear similar to a region of the ventral temporal cortex reported by James and colleagues (2002b) during haptic exploration of 3D objects (but was anterior to the region they found to show visual and haptic priming). Taken with this earlier result, our study suggests that OTS/pFus may be involved in visual form analyses of 3D objects and/or their haptic properties (although in our experiments, haptic and visual stimulation were synchronous and cannot be distinguished).

Summary

Taken together, we found that several areas in the parietal and frontal lobes showed clear grasp- and/or object-specific adaptation, decreases in the fMRI signal that cannot be linked to simple practice effects. Instead, they suggest that both motor programming and processing of the visual stimulus attributes are sensitive to repetition. Furthermore, our results in aIPS and other areas such as mid-SPL are congruent with past studies that observed dorsal stream adaptation with pictures of objects (Rice et al. 2007; Valyear et al. 2006) or movies of objects being grasped (Shmuelof and Zohary 2005). However, now that we know that dorsal stream “priming” is possible with real actions, other attributes expected from macaque physiology (Murata et al. 2000), such as size and orientation, can also be...
investigated. In other words, as in the ventral stream, fMRI adaptation opens the door to new investigations of the human dorsal stream functions that can go beyond the elegant but limited number of investigations in the macaque brain (Murata et al. 2000). Finally, our results can potentially have repercussions for neurophysiologists, who often train the monkeys to perform a very limited number of reach-to-grasp movements. Our study suggests that extensive repeated grasping of the same target with similar movement kinematics could lead to modifications in the neural circuitry such as reduced reponsiveness, sharpened tuning, or faster processing.

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