Graspable objects grab attention when the potential for action is recognized

Todd C. Handy[1,2], Scott T. Grafton[1–3], Neha M. Shroff[1,2], Sarah Ketay[1,2] and Michael S. Gazzaniga[1,2]

[1] *Center for Cognitive Neuroscience,* [2]*Department of Psychological and Brain Sciences, and* [3]*Dartmouth Brain Imaging Center, 6162 Moore Hall, Dartmouth College, Hanover, New Hampshire 03755, USA*

Correspondence should be addressed to: T.C.H. (todd.c.handy@dartmouth.edu)

Published online 17 March 2003; doi:10.1038/nn1031

Visually guided grasping movements require a rapid transformation of visual representations into object-specific motor programs. Here we report that graspable objects may facilitate these visuomotor transformations by automatically grabbing visual spatial attention. Human subjects viewed two task-irrelevant objects—one was a 'tool', the other a 'non-tool'—while waiting for a target to be presented in one of the two object locations. Using event-related potentials (ERPs), we found that spatial attention was systematically drawn to tools in the right and lower visual fields, the hemifields that are dominant for visuomotor processing. Using event-related fMRI, we confirmed that tools grabbed spatial attention only when they also activated dorsal regions of premotor and prefrontal cortices, regions associated with visually guided actions and their planning. Although it is widely accepted that visual sensory gain aids perception, our results suggest that it may also have consequences for object-directed actions.

To what degree can the implicit recognition of an object's motor affordance bias visual attention[1–3]? Viewing tools, pictures of tools, or even the names of tools activates premotor cortex independent of an observer's intention to act[4,5]. This suggests that when a tool's representation is primed by visual input, the motor program used for grasping that tool becomes primed as well[6,7]. Given such interplay between vision and action, it has been debated whether selection for an object-specific motor program has a feedback influence on visual attention[8,9]. To address this issue, we investigated whether implicit recognition of action-related object attributes can lead to an orienting of visual spatial attention to the locations of graspable objects.

Our study design was predicated on an object competition model[10,11]. Participants maintained fixation while two task-irrelevant objects were presented, one in each upper visual hemifield (**Fig. 1a**). The objects were from a canonical set of line drawings[12] and remained on-screen as the participant waited for a target to be superimposed over one of the two objects. Participants were instructed to ignore the objects and make a manual response signaling the target location. The participants did not know that the objects came from two different categories (**Fig. 1b**). The tool category contained the kinds of items previously shown to activate motor schemata in cortex (such as utensils)[4,5]; the non-tool category contained items far less likely to be associated with motor schemata (such as animals). Given the prediction that the activation of an object-specific motor schema will bias cortical processing systems toward that object[13], we asked whether these biases would include an automatic orienting of visual spatial attention to the object's location.

We examined the event-related potentials (ERPs) elicited by the target as a function of trial type: tool-left or tool-right. Spatial attention is reflected in the amplitude of the lateral occipital P1 (positive, early) component of the visual evoked potential: when spatial attention is oriented to a non-foveal location in the visual field, the P1 component elicited by a stimulus in that location is larger in amplitude, relative to when attention is oriented elsewhere in the visual field at the time the stimulus appears[14]. This effect has been attributed to attention-related increases in sensory gain in extrastriate visual cortex[15]. As such, the amplitude of the P1 will parametrically increase with the amount of attention allocated to the location of the ERP-eliciting stimulus[16,17]. Systematic changes in the amplitude of the P1 can thus be interpreted as indicating whether or not spatial attention was oriented to a particular location in the visual field.

The first experiment we report here was based on the P1 measure and showed a visual field asymmetry in the influence of graspable objects on spatial attention. The P1 elicited by targets in the right visual field were larger on tool-right than on tool-left trials, whereas no effect of trial type was observed for targets in the left visual field (**Fig. 2**). A second ERP experiment supported the hypothesis that this asymmetry was linked to right and lower visual hemifield dominance for visuomotor processing. We confirmed this proposal in a third experiment using event-related fMRI, which showed that motor-related regions of premotor and parietal cortices were activated during tool-right but not tool-left trials.

Results

Experiment 1

Twenty-four right-handed volunteers participated. Reaction times (RTs) to the targets are reported in **Table 1** (top), and discrimi-

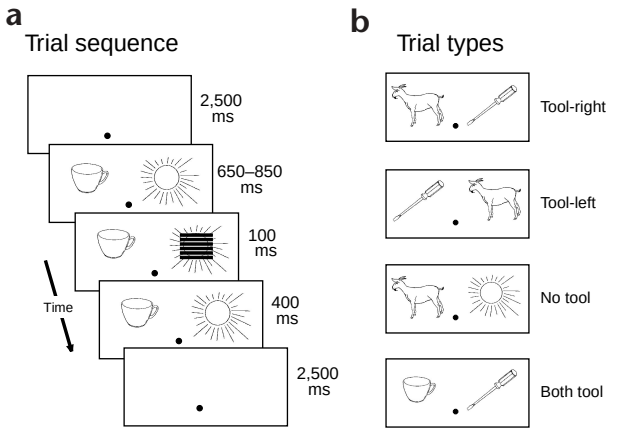

Fig. 1. Display and trial types. The timing and sequence of events on each trial (**a**), and the different trial types, as defined by the tool location in the display (**b**).

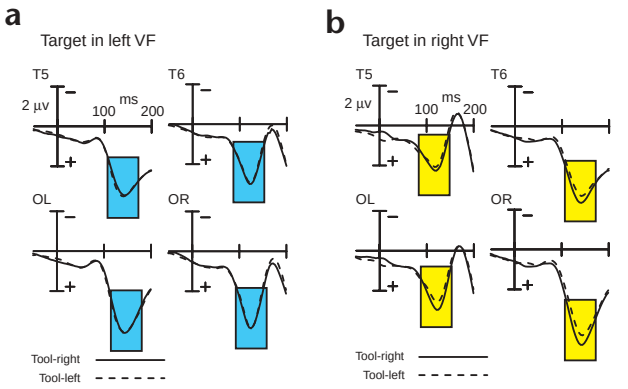

Fig. 2. The lateral occipital P1 by condition from experiment 1, averaged across participants. (**a**) When the target was in the left visual field, the amplitude of the P1 elicited by the target was unaffected by the trial type (blue boxes). (**b**) When the target was in the right visual field, the amplitude of the P1 elicited by the target was larger on tool-right trials, relative to tool-left trials (yellow boxes).

nation accuracy was above 0.90 across all conditions and participants. Measuring the peak amplitude of the lateral occipital P1 elicited by the target (**Fig. 2** and **Table 2**, top), we found an interaction ($F_{1,23} = 11.16$, $P < 0.01$) between the visual field of the target (left versus right) and the trial type (tool present versus absent in the target location). No main effects of target visual field or trial type were observed. These results suggested that there was an increase in sensory gain at the tool location, but only for tools in the right visual field.

Experiment 2

We hypothesized that the visual field asymmetry in experiment 1 might be tied to the functional neuroanatomy underlying action-related processes in cortex. In particular, the representation and planning of motor actions show a lateralization to the left cerebral hemisphere[18,19]. In the context of a bilateral display, this suggests that a right visual field advantage may exist for the recognition of action-related object attributes[20]. However, action-related asymmetries are not limited to the lateral visual hemifields—there is also a lower hemifield advantage in directing visually guided actions relative to the upper hemifield[21]. This suggested that we could replicate the basic result of experiment 1 while predicting an asymmetry in gain effects favoring the lower visual hemifield. To test this possibility, we conducted a second ERP experiment that differed from the first only in that the object locations were centered above and below fixation on the vertical meridian. The trial types of interest were thus 'tool-upper' and 'tool-lower', with the prediction that there should be a greater effect of the tool on sensory gain on tool-lower trials.

Thirteen right-handed volunteers participated. RTs to the targets are reported in **Table 1** (middle), and discrimination accuracy was above 0.85 across all conditions and participants. Measuring the P1 elicited by the target (**Fig. 3** and **Table 2**, bottom), an interaction was again found ($F_{1,12} = 8.61$; $P < 0.05$) between the visual field of the target (upper versus lower) and the trial type (tool present versus absent in the target location). There was also a main effect of target visual field ($F_{1,12} = 18.66$; $P < 0.001$), indicating an overall larger P1 in the upper visual field. No main effect of trial type was found. Although gain seemed to be increased at the tool location in both visual hemifields, the effect was biased toward the lower hemifield. These results were thus consistent with the proposal that the asymmetry observed in experiment 1 was at least partially driven by known visual field asymmetries in visuomotor processing.

Table 1. Mean reaction times (in ms) by experiment, averaged across participants.

Experiment	Visual field of target	Location of tool in display		Significant effects*
		Tool-left	Tool-right	
1	Left	287	286	
(ERP)				None
	Right	285	284	
		Tool-upper	Tool-lower	
2	Upper	371	377	
(ERP)				VF
	Lower	374	364	Tool × VF
		Tool-left	Tool-right	
3	Left	412	421	
(fMRI)				None
	Right	422	413	

*Effects are reported at $P < 0.05$. VF, visual field.

Experiment 3

We then wanted to confirm that spatial attention was drawn toward graspable objects in the right but not left visual field because of a right visual field advantage in the processing of object-specific motor affordances. An alternative explanation is that the asymmetry in the P1 effect, as observed in experiment 1, could have simply resulted from cerebral hemispheric asymmetries in the sensory-level processing of different spatial frequencies. Although the spatial frequency of the target itself remained constant across all trial types, we could not eliminate the possibility that low-level interactions between the target and the object type over which the target was superimposed (tool versus non-tool) may have systematically altered the effective spatial frequency of the target at the time of its presentation (for example, due to overlapping features). The concern here is that interactions occur between the spatial frequency of an ERP-eliciting stimulus and the cerebral hemisphere from which an

ERP is recorded that systematically affect the morphology of sensory-evoked ERP components[22,23]. One could thus postulate that the results from experiment 1 had their causal explanation rooted in hemispheric asymmetries in the sensory processing of specific spatial frequencies, rather than as an effect attributable to visual field asymmetries in visuomotor processing.

Importantly, these competing possibilities could be directly tested using fMRI. If motor affordances were being preferentially recognized in the right visual hemifield, activation in motor-related regions of cortex should be greater on tool-right trials than on tool-left trials[4,5]. Conversely, such a data pattern would not be expected if the findings from experiment 1 were simply driven by sensory-level spatial frequency confounds. To resolve this issue, we carried out a third experiment using event-related fMRI in a task design that was essentially identical to that used in experiment 1, but with the following exceptions: (i) targets were presented on only 28.5% of the trials to allow us to restrict data analysis to trials that did not engender a manual response, and (ii) equal numbers of tool-left, tool-right, no-tool and both-tool trials were included to facilitate direct statistical comparisons between trials with and without tools in the display.

Fourteen right-handed volunteers participated. RTs to the targets are reported in **Table 1** (bottom), and discrimination accuracy was above 0.95 across all trial types and participants.

Table 2. Peak amplitude of the P1 ERP component from experiments 1 and 2, averaged across participants (in μV ± s.e.m.)*.

Experiment 1

		Location of tool in display	
Visual field of target	Electrode	Tool-left	Tool-right
Left	OL	4.16 ± 0.31	4.14 ± 0.31
	OR	3.90 ± 0.38	3.95 ± 0.36
	T5	3.52 ± 0.32	3.61 ± 0.29
	T6	3.01 ± 0.30	3.10 ± 0.29
Right	OL	2.66 ± 0.36	3.03 ± 0.34
	OR	4.40 ± 0.27	4.91 ± 0.32
	T5	2.21 ± 0.33	2.34 ± 0.33
	T6	3.59 ± 0.25	3.94 ± 0.27

Experiment 2

		Location of tool in display	
Visual field of target	Electrode	Tool-upper	Tool-lower
Upper	OL	4.54 ± 0.61	4.92 ± 0.68
	OR	4.78 ± 0.45	5.08 ± 0.52
	T5	3.31 ± 0.48	3.71 ± 0.53
	T6	3.39 ± 0.25	3.68 ± 0.33
Lower	OL	2.54 ± 0.43	2.88 ± 0.35
	OR	1.56 ± 0.49	2.17 ± 0.39
	T5	2.22 ± 0.26	2.50 ± 0.25
	T6	1.62 ± 0.39	2.27 ± 0.37

*Values were measured relative to a 200 ms pre-stimulus baseline.

Analysis of the fMRI blood oxygen level–dependent (BOLD) signal was based on a regions of interest (ROI) approach. Our ROI criterion followed from three lines of evidence. First, both ventral (PMv) and dorsal (PMd) premotor cortices have been shown to activate when viewing pictures of tools, an effect linked to the visual priming of object-specific motor schemata[4,5]. Second, it is believed that PMd and the prefrontal region immediately rostral to PMd (pre-PMd) are integral to higher-level aspects of action and its planning, including the formation of visuomotor associations[24]. Third, our model stipulated that visuomotor processing influences the orienting of spatial attention. Given that both visuomotor[25,26] and attentional control[27,28] networks include projections from precentral brain regions to parietal cortex, our model predicted that we should see a significantly greater BOLD response in parietal cortex on tool-right relative to tool-left trials. As a result, we restricted consideration of the fMRI data to voxel clusters in these regions of prefrontal, premotor and parietal cortices.

We first determined the regions of cortex showing an event-related BOLD response for each of the three trial types of interest, respectively: tool-left, tool-right and no-tool (data from both-tool trials were not analyzed because any ROI activations on these trials could not be uniquely attributed to a specific tool). The only significant ROI voxel clusters were found bilaterally in the PMd and intraparietal lobule (IPL) and in right pre-PMd during tool-right trials (**Fig. 4** and **Table 3**). To isolate ROI activity uniquely associated with tools, we then directly compared the BOLD response on tool-left and tool-right trials, respectively, to the no-tool trials. Significant voxel clusters were found bilaterally in the PMd/pre-PMd regions and in right IPL in the tool-right > no-tool contrast, and in the left PMd region in the tool-left > no-tool contrast (**Fig. 5a** and **Table 3**). As a final analysis, we directly compared BOLD responses on the tool-left and tool-right trials. This pair of contrasts revealed that bilateral regions of pre-PMd and IPL cortex had significantly larger BOLD responses during tool-right trials relative to tool-left trials, whereas only a small cluster in the medial premotor (or pre-SMA) region had a significantly larger BOLD response during tool-left trials relative to tool-right trials

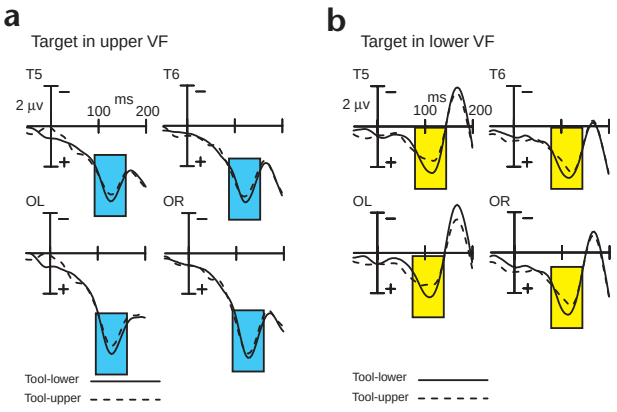

Fig. 3. The lateral occipital P1 by condition from experiment 2, averaged across participants. (**a**) When the target was in the upper visual field, the amplitude of the P1 elicited by the target appeared larger on tool-lower relative to tool-upper trials (blue boxes). (**b**) When the target was in the lower visual field, the amplitude of the P1 elicited by the target was significantly larger on tool-lower trials, relative to tool-upper trials (yellow boxes).

Table 3. Significant voxel clusters in prefrontal, premotor and parietal cortices from experiment 3.

	Talairach coordinates[50]					Anatomical locus	
Contrast	*x*	*y*	*z*	*k*	*t*	BA	Gyrus
Tool-right >	–12	21	34	32	6.14	32	Left anterior cingulate
Baseline	51	19	30	121	5.73	9	Right middle frontal
	–44	8	46	30	5.45	6	Left middle frontal
	–4	19	36	10	4.71	32	Left anterior cingulate
	53	–51	32	123	5.91	40	Right IPL
	–53	–50	32	60	5.57	40	Left IPL
Tool-left >	–28	–5	65	17	4.66	6	Left superior frontal
no tool	–6	10	47	10	4.46	6	Left medial frontal
Tool-right >	36	21	40	70	6.45	8	Right middle frontal
no tool	36	4	48	17	6.45	6	Right middle frontal
	22	–6	44	29	5.89	6	Right middle frontal
	–57	7	29	16	5.43	6	Left precentral
	–8	6	44	16	4.75	24	Left anterior cingulate
	–44	8	46	21	4.63	6	Left middle frontal
	50	–37	33	32	5.50	40	Right IPL
	42	–42	45	15	4.67	40	Right IPL
Tool-left > tool-right	2	11	58	14	4.85	6	Right superior frontal
Tool-right >	–14	31	33	1323	9.56	6	Left medial frontal
tool-left	28	16	49	1208	6.43	8	Right superior frontal
	16	11	34	10	4.40	32	Right anterior cingulate
	57	–33	48	31	5.97	40	Right postcentral
	–42	–41	33	100	5.86	40	Left IPL
	53	–56	42	207	5.32	40	Right IPL

There were no significant clusters in the ROIs in the tool-left > baseline contrast. The *t*-values are for the statistical maxima within each cluster, the minimum cluster size reported (k) was 10 voxels, and all contrasts are reported at $P < 0.001$ (uncorrected). BA, Brodmann's area; IPL, inferior parietal lobule.

(**Fig. 5b** and **Table 3**). In sum, given that the spatial extent of ROI activity was significantly greater during tool-right relative to tool-left trials at all three levels of analysis, the data thus supported the proposal that the visual field asymmetry observed in experiment 1 could be explained in relation to a right visual field advantage in visuomotor processing.

Discussion

Our ERP findings converge on the conclusion that graspable objects have the capacity to draw visual spatial attention to their locations, even if those objects are irrelevant to current behavioral goals. However, spatial attention was only drawn to tools when they were in the right visual hemifield. We hypothesized that this laterality was associated with visual field asymmetries in the processing of action-related object attributes, a possibility supported by our event-related fMRI data. The collective results thus suggest that the implicit recognition of action-related object attributes can bias object competition—and visual spatial attention—toward graspable objects[13]. From a broader perspective, the effects of spatial attention on visual sensory gain have previously been associated with factors such as willful decisions about where to orient attention[29], sudden events that capture attention[30] and perceptual task demands that narrow the focus of attention[31]. It now appears that visuomotor biases are also capable of modulating location-specific visual sensory gain.

Given these conclusions, a number of important questions follow. First, if motor affordances were being implicitly recognized in the tools, what is the underlying nature of the recognition process? It has been proposed that recognition involves activating semantic knowledge of motor use that has been linked to an object representation through experience[4–7]. However, it is also possible that recognition of affordances may not completely depend on object-specific motor knowledge. Indeed, although the tool and non-tool objects were equated for complexity and familiarity (Methods), a comparison of the mean images of these two object categories revealed that tools tended to be, on average, long and narrow in shape while non-tools tended to be more symmetrical about their central axis. This raises the possibility that recognition of a motor affordance may occur for any object that conforms to a grasp-appropriate shape, independent of whether or not that object has been previously associated with an idiosyncratic motor pattern. If so, it becomes interesting to consider whether right visual field advantages in visuomotor processing may be influenced by cerebral asymmetries in processing spatial frequencies, with the left hemisphere preferring higher spatial frequencies relative to the right[32].

Second, under conditions where the ERP data indicated that attention had been oriented to the tool location, why were attention effects not always observed in the RT data? In particular, orienting visual attention to a spatial location typically decreases RTs to targets in that location, relative to targets presented in unattended locations[33]. Instead, however, we found a dissociation between the ERP and RT data. Given that action-related objects will activate motor schemata specific to their use, we suspect that RTs were being affected by response interference between the activated motor schema and the need to make a

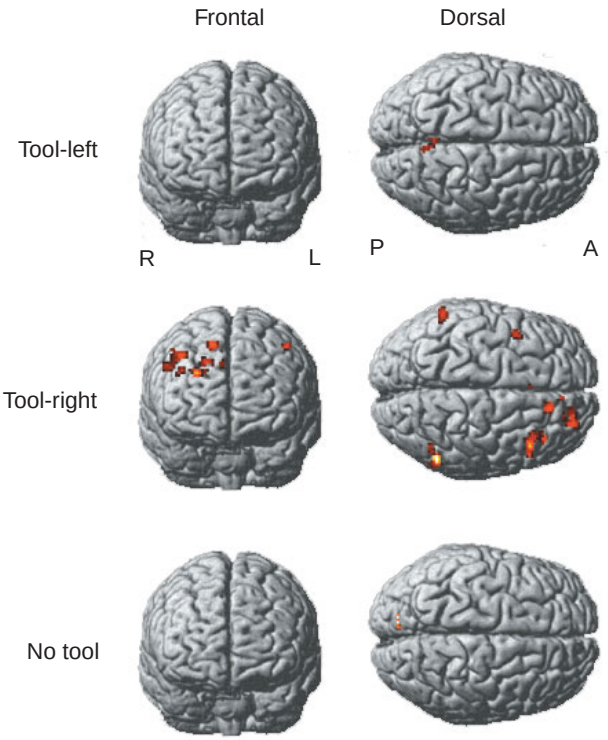

Fig. 4. fMRI BOLD response as a function of trial type, averaged across participants. Data are shown on the single-subject rendered brain provided with SPM99, thresholded at $P < 0.001$ (uncorrected), with a minimum cluster size of 10 voxels. Significant voxel clusters were found in PMd, pre-PMd and IPL on tool-right trials only. Statistics and coordinates for all relevant clusters are reported in **Table 3**. R, right; L, left; A, anterior; P, posterior.

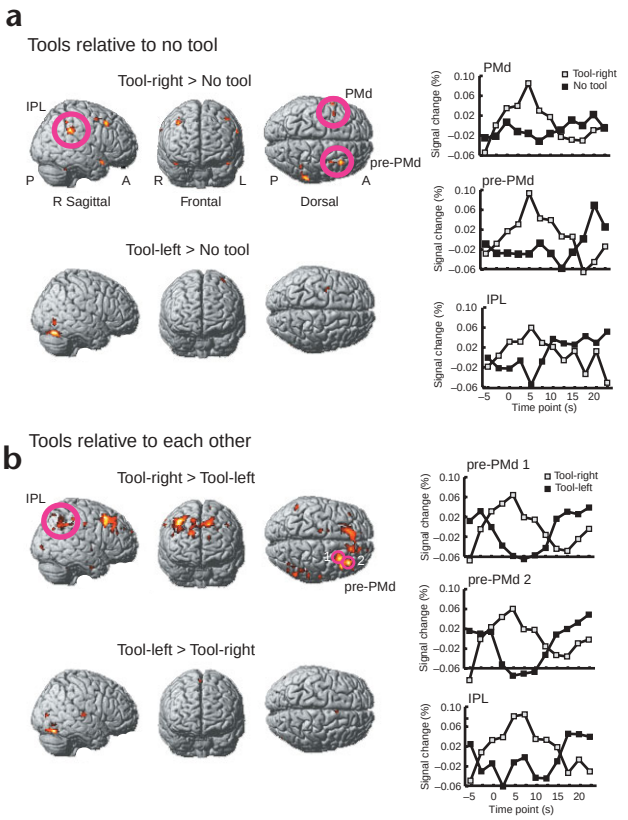

Fig. 5. fMRI BOLD response as a function of contrast, averaged across participants. Data are shown on the single-subject rendered brain provided with SPM99 (thresholded at $P < 0.001$ (uncorrected), with a minimum cluster size of 10 voxels). (**a**) Areas showing a larger BOLD response on tool-left and tool-right trials, relative to no-tool trials (left). On the right are plotted the percent signal change as a function of trial type within the clusters circled in the tool-right > no-tool contrast on the left. These plots suggest that the differential effect in these clusters was driven by a response only in the tool-right trials. (**b**) Areas showing a larger BOLD response on tool-right trials relative to tool-left trials, and vice-versa (left). On the right are plotted the percent signal change as a function of trial type within the clusters circled in the tool-right > no-tool trials. These plots suggest that the differential effect in these clusters was driven by both an increased response on tool-right trials and an inhibitory response on tool-left trials. Statistics and coordinates for all relevant clusters are reported in **Table 3**. R, right; L, left; A, anterior; P, posterior.

manual response that, in all likelihood, was incompatible with that schema. Consistent with this possibility, recent ERP evidence has shown that RTs to targets at attended locations may show no evidence of attentional facilitation if the target requires an unexpected response, even though systematic modulations in P1 amplitude indicate that there was an increase in sensory gain at the target's location[34].

Third, if visuomotor processes are influencing visual sensory gain, what is the cortical network underlying this modulatory capacity? Attention to motor planning has been linked to activity in the left anterior supramarginal gyrus of the IPL[19,35]. Not only do the results from experiment 3 indicate that this region was activated under conditions associated with increased sensory gain at the tool location, but the homologous region in the right cerebral hemisphere was involved as well. Interestingly, however, these bilateral IPL activations were more inferior and anterior to the parietal regions typically associated with the volitional control of spatial attention[27,28]. This suggests that although spatial attention was being influenced by graspable objects in the right visual field, the effect did not depend on engaging more dorsal parietal regions subserving the top-down control of attentional orienting. Our data are thus consistent with the proposal that visuospatial attention is labile to modulation by two dissociable parietal-premotor networks, one linked to executive attentional control and one to motor-related influences—a proposal that has been previously supported by neuropsychological evidence[36–38].

Fourth, what are the different levels at which visual selective attention may interact with visuomotor processing? On the one hand, the motor affordance of an object must first be recognized, a process that likely involves attention to specific object features. For example, the ability of a parietal patient to use action-defined targets to perform a visual search task is reduced when the target object in question has a handle that is oriented away from the patient[39]. This and related findings in normal subjects[3] indicate that feature-level attention clearly interacts with motor affordance recognition. In turn, it seems that once a motor affordance is recognized, this can affect attentional selection at the level of whole objects. Visual extinction patients, for instance, are more likely to report awareness of two objects in a display if those objects are spatially arranged in a manner consistent with their combined use (a corkscrew near the top rather than the bottom of a bottle)[38]. Our findings are consistent with visuomotor-driven

selection at this level. When the tool's motor affordance was recognized in the right visual field (experiment 3), this was associated with selection for objects in that location as measured by systematic increases in visual sensory gain (experiment 1).

Finally, why might visual sensory gain be susceptible to modulation by visuomotor processing? Gain control has typically been linked to perceptual acuity[15,26], yet vision subserves action as well as perception[40]. Taken in this light, our data suggest that sensory gain may have consequences for both aspects of vision. Object-oriented visuomotor transformations require making a series of non-trivial computations in rapid succession: both egocentric and allocentric spatial reference frames must be established[41], grip aperture must be scaled to the size and shape of the object[42,43], and the reaching movements used to bring the hand to an object must be accurately programmed[44–46]. Increased sensory gain may not only aid visual perception *per se*, but it may also facilitate the programming of these action-related parameters once a graspable object has been recognized and has drawn attention to its location.

Methods

Task design. All procedures and protocols were approved by the Committee for the Protection of Human Subjects at Dartmouth College, and all participants gave their informed written consent. Stimulus timing parameters for experiments 1 and 2 are shown in **Fig. 1**. Stimuli were presented on a color video monitor using VAPP stimulus presentation software (http://nilab.psychiatry.ubc.ca/vapp/). Participants signaled the target location by making a button press with the left thumb for targets in the left (and upper) visual hemifield, and by a button press with the right thumb for targets in the right (and lower) visual hemifield. Participants were run in a total of 15 trial blocks of 64 trials each. Half of the trials in each run had a short interval between object and target presentation (SOA of 100–300 ms instead of 650–850 ms), a control condition included to ensure that participants would immediately attend to the stimulus display once the objects were presented (see below). Within each run, there were 24 trials each of the tool-left/upper and tool-right/lower trials, and 8 trials each of the no-tool and both-tool trials, equally split between the two SOA conditions. Trial numbers were skewed toward the tool-left and tool-right trials to maximize the signal-to-noise ratio of the target ERPs elicited on these trials. Targets were presented on every trial and appeared with equal frequency over the left and right objects within each run and within each trial type. The objects and target were presented in black against a gray background. The target was a square wave grating of 2 cycles/°, forming an approximately 1° square. The objects were from a well-known set of black-and-white line drawings[12], never exceeded ~2° in width or height, and were presented ~3° from center fixation in the given visual hemifield. There were 50 different objects in each of the two object categories, and based on ratings provided with the original reference[12], tools and non-tools were equated for complexity (2.49 versus 2.59, respectively) and familiarity (both 3.60). Scales for both familiarity and complexity were from 1 (very unfamiliar, very simple) to 5 (very familiar, very complex). On each trial, the appropriate objects were randomly drawn from their category with replacement. Importantly, post-experiment debriefing confirmed that all participants remained naive as to the distinction in object categories.

The following changes were made to the above paradigm to accommodate event-related fMRI. Each participant performed six functional runs. Each functional run began and ended with 20 s of fixation-only 'rest' and had a total of 84 trials equally divided among tool-left, tool-right, no-tool and both-tool trials; 24 of these trials (28.5%) had targets (three targets for each combination of trial type and target location). Randomly interspersed with the trials were 27 fixation-only intervals equally split among one, two and three TRs in duration. Finally, only one object-target SOA was used (750 ms) in order to maximize the number of trials used for estimating the event-related hemodynamic response for each trial type.

ERP recording and analysis. Scalp potentials were recorded from a 17-electrode array mounted in the posterior region of a custom elastic cap. All electroencephalographic (EEG) activity was recorded relative to the left mastoid, amplified at a gain of 50,000 with a band-pass of 0.1–30 Hz (half-amplitude cutoffs) using a Grass Instruments (Quincy, Massachusetts) Model 12 Neurodata Acquisition System, and digitized on-line at a sampling rate of 256 samples/s. To ensure proper eye fixation, vertical and horizontal electro-oculograms (EOGs) were also recorded, the vertical EOG from an electrode inferior to the right eye, and the horizontal EOG from electrodes on the outer canthi. All electrode impedances were kept below 5 kΩ throughout recording. Off-line, computerized artifact rejection was used to eliminate trials during which detectable eye movements (>1°), blinks, muscle potentials or amplifier blocking occurred. For each subject, ERPs for each condition of interest were averaged into 3,000 ms epochs, beginning 1,500 ms before the onset of the time-locking stimulus. Subsequently, all ERPs were algebraically re-referenced to the average of the left and right mastoid signals, convolved with a low-pass Gaussian filter (25.6 Hz half-amplitude cutoff) to eliminate high-frequency artifacts in the waveforms, and convolved with a single-pole high-pass filter to remove slow drift and DC components. Statistical analyses were restricted to the data from lateral occipital scalp sites OL, OR, T5 and T6, the locations where the visually-evoked P1 is maximal. A repeated-measures ANOVA was performed, based on measuring—for each target location, trial type and electrode site—the amplitude of single-subject P1s at the latency of the P1 peak in the grand-averaged waveform. All amplitude measures were relative to a 200 ms pre-stimulus baseline; separate analyses of these baselines showed that baseline variances did not statistically differ between conditions of interest. ERP waveforms for the targets from the short SOA conditions were not analyzed because of excessive response overlap from the temporally adjacent presentation of the objects.

fMRI recording and analysis. fMRI data were collected using a 1.5T Signa scanner (GE Medical Systems, Milwaukee, Wisconsin) with a fast gradient system for echo-planar imaging (EPI). Dense foam padding was used for head stabilization. Scanning was performed in a darkened room, with visual images rear-projected to a screen behind the participant's head and viewed via a headcoil-mounted mirror. EPI images were acquired using a gradient-echo pulse sequence and interleaved slice acquisition (TR = 2,500 ms, TE = 35 ms, flip angle = 90°, 25 contiguous slices at 4.5 mm skip 1 mm, in-plane resolution of 64 × 64 pixels in a FOV of 24 cm). Each functional run began with four 2 s 'dummy' shots to allow for steady-state tissue magnetization. A total of 172 EPI volumes were collected in each functional run. High-resolution, T1-weighted axial images were also taken of each subject (TR = 25 ms, TE = 6 ms, bandwidth = 15.6 kHz, voxel size = 0.9375 × 1.25 × 1.2 mm). The beginning of each trial and fixation-only interval was synchronized to the onset of acquisition for each EPI volume. Data were processed and analyzed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). For each subject, the EPI images were corrected for slice timing before correction for motion[47]. The EPI and anatomical images were then co-registered and spatially normalized into MNI stereotaxic coordinates using the filT1.img template provided with SPM99[48]. After normalization, the EPI images were spatially smoothed using an isotropic 12 mm Gaussian kernel.

The smoothed, normalized single-subject data were analyzed via multiple regression using the general linear model[49]. In the regression model, the six functional runs were treated as a single run with separate linear, quadratic and cubic regressors included as effects of non-interest for each of the actual functional runs. Mean (or DC) differences between functional runs were regressed out by including a constant regressor for five of the six functional runs. As effects of interest, regressors were included both for each trial type with targets and for each trial type without targets, all modeled on the canonical event-related hemodynamic response function; regressors for temporal derivatives of each of these trial types were also included. Group-level analyses were based on a random-effects model using one-sample *t*-tests. Although the experiment was based on an ROI approach, no small-volume correction was used during statistical analysis.

Acknowledgments

This study was supported by funding from the National Institute of Health and Dartmouth College. We thank D. Turk, W. Kelley, E. R. Matheney and S. Mann for technical assistance.

Competing interests statement

The authors declare that they have no competing financial interests.

RECEIVED 8 JANUARY; ACCEPTED 10 FEBRUARY 2003

1. Craighero, L., Fadiga, L., Umilta, C.A. & Rizzolatti, G. Evidence for visuomotor priming effect. *Neuroreport* **8**, 347–349 (1996).
2. Jeannerod, M., Arbib, M.A., Rizzolatti, G. & Sakata, H. Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci*. **18**, 314–320 (1995).
3. Tucker, M. & Ellis, R. On the relations between seen objects and components of potential actions. *J. Exp. Psychol. Hum. Percept. Perform.* **24**, 830–846 (1998).
4. Chao, L.L. & Martin, A. Representation of manipulable man-made objects in the dorsal stream. *Neuroimage* **12**, 478–484 (2000).
5. Grafton, S.T., Fadiga, L., Arbib, M.A. & Rizzolatti, G. Premotor cortex activation during observation and naming of familiar tools. *Neuroimage* **6**, 231–236 (1997).
6. Martin, A., Haxby, J.V., Lalonde, F.M., Wiggs, C.L. & Ungerleider, L.G. Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* **270**, 102–105 (1995).
7. Martin, A., Wiggs, C.L., Ungerleider, L.G., & Haxby, J.V. Neural correlates of category-specific knowledge. *Nature* **379**, 649–652 (1996).
8. Bonfiglioli, C., Duncan, J., Rorden, C. & Kennett, S. Action and perception: evidence against converging selection processes. *Vis. Cognit.* **9**, 458–476 (2002).
9. Craighero, L., Fadiga, L., Rizzolatti, G. & Umiltà, C. Action for perception: a motor-visual attentional effect. *J. Exp. Psychol. Hum. Percept. Perform.* **25**, 1673–1692 (1999).
10. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193–222 (1995).
11. Duncan, J., Humphreys, G. & Ward, R. Competitive brain activity in visual attention. *Curr. Opin. Neurobiol.* **7**, 255–261 (1997).
12. Snodgrass, J.G. & Vanderwart, M. A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity and visual complexity. *J. Exp. Psychol. Hum. Learn. Mem.* **6**, 174–215 (1980).
13. Ward, R. Interaction between perception and action systems: a model for selective action. in *Attention, Space and Action: Studies in Cognitive Neuroscience* (eds. Humphreys, G.W., Duncan, J. and Treisman, A.) 311–332 (Oxford Univ. Press, New York, 1999).
14. Van Voorhis, S. & Hillyard, S.A. Visual evoked potentials and selective attention to points in space. *Percept. Psychophys.* **23**, 146–160 (1977).
15. Hillyard, S.A., Vogel, E.K. & Luck, S.J. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. in *Attention, Space and Action: Studies in Cognitive Neuroscience* (eds. Humphreys, G.W., Duncan, J. and Treisman, A.) 311–332 (Oxford Univ. Press, New York, 1999).
16. Handy, T.C. & Mangun, G.R. Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. *Percept. Psychophys.* **62**, 175–186 (2000).
17. Mangun, G.R. & Hillyard, S.A. Spatial gradients of visual attention: behavioral and electrophysiological evidence. *Electroencephal. Clin. Neurophysiol.* **70**, 417–428 (1988).
18. Haaland, K.Y. & Harrington, D.L. Hemispheric asymmetry of movement. *Curr. Opin. Neurobiol.* **6**, 796–800 (1996).
19. Rushworth, M.F.S., Krams, M. & Passingham, R.E. The attentional role of the left parietal cortex: the distinct lateralization and localization of motor attention in the human brain. *J. Cogn. Neurosci.* **13**, 698–710 (2001).
20. Boles, D.B. An experimental comparison of stimulus type, display type and input variable contributions to visual field asymmetry. *Brain Cogn.* **24**, 184–197 (1994).
21. Danckert, J. & Goodale, M.A. Superior performance for visually guided pointing in the lower visual field. *Exp. Brain Res.* **137**, 303–308 (2001).
22. Kenemans, J.L., Baas, J.M.P., Mangun, G.R., Lijffijt, M. & Verbaten, M.N. On the processing of spatial frequencies as revealed by evoked-potential source modeling. *Clin. Neurophysiol.* **111**, 1113–1123 (2000).
23. Zani, A. & Proverbio, A.M. Attention modulation of short latency ERPs by selective attention to conjunction of spatial frequency and location. *J. Psychophysiol.* **11**, 21–32 (1997).
24. Picard, N. & Strick, P.L. Imaging premotor areas. *Curr. Opin. Neurobiol.* **11**, 663–672 (2001).
25. Marconi, B. *et al.* Eye-hand coordination during reaching. I. Anatomical relationships between parietal and frontal cortex. *Cereb. Cortex* **11**, 513–527 (2001).
26. Battaglia-Mayer, A. *et al.* Eye-hand coordination during reaching. II. An analysis of the relationships between visuomanual signals in parietal cortex and parieto-frontal association projections. *Cereb. Cortex* **11**, 528–544 (2001).
27. Corbetta, M. & Shulman, G.L. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3**, 201–215 (2002).
28. Hopfinger, J.B., Buonocore, M.H. & Mangun, G.R. The neural mechanisms of top-down attentional control. *Nat. Neurosci.* **3**, 284–291 (2000).
29. Luck, S.J. *et al.* Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *J. Exp. Psychol. Hum. Percept. Perform.* **20**, 887–904 (1994).
30. Hopfinger, J.B. & Mangun, G.R. Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychol. Sci.* **9**, 441–446 (1998).
31. Handy, T.C., Soltani, M. & Mangun, G.R. Perceptual load and visuocortical processing: ERP evidence of sensory-level selection. *Psychol. Sci.* **12**, 213–218 (2001).
32. Ivry, R.B. & Robertson, L.C. *The Two Sides of Perception* (MIT Press, Cambridge, Massachusetts, 1998).
33. Posner, M.I. Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3–25 (1980).
34. Handy, T.C., Green, V., Klein, R. & Mangun, G.R. Combined expectancies: ERPs reveal the early benefits of spatial attention that are obscured by reaction time measures. *J. Exp. Psychol. Hum. Percept. Perform.* **27**, 303–317 (2001).
35. Rushworth, M.F.S., Ellison, A. & Walsh, V. Complementary localization and lateralization of orienting and motor attention. *Nat. Neurosci.* **4**, 656–661 (2001).
36. Hodges, J.R., Spatt, J. & Patterson, K. "What" and "how": evidence for the dissociation of object knowledge and mechanical problem-solving skills in the human brain. *Proc. Natl. Acad. Sci. USA* **96**, 9444–9448 (1999).
37. Humphreys, G.W. & Riddoch, M.J. Knowing what you need but not what you want: affordances and action-defined templates in neglect. *Behav. Neurol.* **13**, 75–87 (2001).
38. Riddoch, M.J., Humphreys, G.W., Edwards, S., Baker, T. & Willson, K. Seeing the action: neuropsychological evidence for action-based effects on object selection. *Nat. Neurosci.* **6**, 82–89 (2003).
39. Humphreys, G.W. & Riddoch, M.J. Detection by action: neuropsychological evidence for action-defined templates in search. *Nat. Neurosci.* **4**, 84–88 (2001).
40. Milner, A.D. & Goodale, M.A. *The Visual Brain in Action* (Oxford Univ. Press, New York, 1995).
41. Colby, C.L. Action-oriented spatial reference frames in cortex. *Neuron* **20**, 15–24 (1998).
42. Marotta, J.J. & Goodale, M.A. The role of familiar size in the control of grasping. *J. Cogn. Neurosci.* **13**, 8–17 (2001).
43. Murata, A., Gallese, V., Luppino, G., Kaseda, M. & Sakata, H. Selectivity for the shape, size and orientation of objects for grasping in neurons of monkey parietal area AIP. *J. Neurophysiol.* **83**, 2580–2601 (2000).
44. Batista, A.P. & Andersen, R.A. The parietal reach region codes the next planned movement in a sequential reach task. *J. Neurophysiol.* **85**, 539–544 (2001).
45. Carey, D.P. Eye-hand coordination: eye to hand or hand to eye? *Curr. Biol.* **10**, 416–419 (2000).
46. Graziano, M.S.A. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc. Natl. Acad. Sci. USA* **96**, 10418–10421 (1999).
47. Friston, K.J. *et al.* Spatial registration and normalization of images. *Hum. Brain Mapp.* **2**, 165–189 (1995).
48. Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.-P., Frith, C.D., & Frackowiak, R.S.J.,statistical parametric maps in functional imaging: a general linear approach. *Human Brain Mapp.* **2**, 189–210 (1995b).
49. Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S. & Turner, R. Movement-related effects in fMRI time-series. *Magn. Reson. Med.* **35**, 346–355 (1996).
50. Talairach, J. & Tournoux, P. *Co-planar Stereotaxic Atlas of the Human Brain* (Thieme, New York, 1988).