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Placing a tool in the spotlight: spatial attention modulates visuomotor responses in cortex

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Visual spatial attention has long been associated with facilitatory effects on visual perception. Here, we report that spatial attention can also modulate implicit visuomotor processing in dorsal regions of human cortex. Participants underwent fMRI scanning while performing a voluntary attentional orienting task that varied the category of a task-irrelevant object in the attended location (tool vs. non-tool). Data were then analyzed as a function of the attended location (left vs. right visual field) and the object category in that location. We found that the fMRI BOLD response in two visuomotor-related regions–the supplementary motor area (SMA) and the left inferior parietal lobule (IPL)–showed an interaction between the location of attention and the location of the tool in the bilateral display. Further, these responses were statistically distinct from those regions in dorsal cortex showing activity modulated only by the tool location or only by the attended location. While the effects of attending non-foveally within the visual field have been well documented in relation to visual perception, our findings support the proposal that voluntary visuospatial attention may also have consequences for the implicit planning of object-directed actions.

To what extent can spatial attention facilitate the automatic responses that occur in visuomotor cortex when a graspable object such as a cup or utensil comes into view? At issue is whether the modulatory effects of spatial attention–long identified as enhancing stimulus processing in the ventral, perception-related visual pathway (for a review, see Handy et al., 2001)–extend to visuomotor processes in the dorsal, action-related visual pathway (e.g., Milner and Goodale, 1995). The possibility that it may stems from the abundance of behavioral evidence showing consistent motor-related influences on visual attention (e.g. Bonfiglioli et al., 2002; Craighero et al., 1999; Deubel et al., 1998; Humphreys and Riddoch, 2001; Pavese and Buxbaum, 2002; Riddoch et al., 2003; Rizzolatti et al., 1994; Tipper et al., 1992; Tucker and Ellis, 1998, 2004; Ward, 1999; Weir et al., 2003). Further, recent neuroimaging data have suggested that when a graspable object generates a visuomotor response (VMR) in cortex, it can implicitly bias spatial attention towards the location of that object (Handy et al., 2003). Yet whether the reciprocal relationship exists–with spatial attention modulating the VMR generated by a graspable object–remains unknown. We investigated this question in the following study using event-related fMRI.

Our experiment was predicated on examining object-specific VMRs as a function of whether or not spatial attention was voluntarily oriented to the object's location at the time of presentation. In turn, our operational definition of a VMR followed from neuroimaging evidence showing that a number of different visuomotor-related areas in cortex may automatically respond when a graspable object such as a tool comes into view (see Picard and Strick, 2001). Depending on conditions, these areas have included both dorsal and ventral premotor cortex (PMd and PMv), the region just anterior to PMd (prePMd), the supplementary motor area (SMA), the region just anterior to SMA (preSMA), and the inferior parietal lobule (IPL) (e.g., Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2002; Grèzes et al., 2003; Jeannerod, 2001). Operationalizing VMRs in relation to activity in these visuomotor areas, we recently found that when a tool was presented in the right visual field (RVF) location of a bilateral display, a VMR was observed in bilateral prePMd and bilateral IPL (Handy et al., 2003). In contrast, when the object locations were switched such that the tool was in the left visual field (LVF) location of the display, no such VMR was generated. Building on this initial result–which did not include an overt manipulation of voluntary attentional orienting–the current goal was to characterize the VMR generated by a lateralized tool as a function of (1) its visual field location and (2) whether or not attention was voluntarily oriented to that location at the time of the tool's presentation. If the modulatory effects of spatial attention extend to the dorsal/action visual pathway, it predicted that the VMR generated by a tool would vary depending on whether or not the tool's location was covertly attended.

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To test this prediction, participants underwent fMRI scanning while performing a visuospatial attention task (Fig. 1). On each trial, an object was displayed on either side of fixation, one object always a tool (e.g., a utensil) and the other always a non-tool (e.g., a seahorse). Prior to the appearance of these objects, a cue was presented at fixation that indicated the location of an upcoming target that–if present on that trial–would be superimposed over the object in the cued location. Only the object locations were thus relevant to the task. Participants were instructed to hold central fixation while covertly orienting their attention to the cued location. Importantly, eye position was monitored during scanning to confirm that fixation was maintained. Data analysis then centered on examining the event-related fMRI responses to the onset of the object displays on non-target trials as a joint function of the location of attention (left vs. right visual field) and the type of object in the attended location (tool vs. non-tool).

Materials and methods

Participants

Twenty-one right-handed volunteers were paid to participate in the study (11 female, 10 male, age: 19–29 years old). All were neurologically normal, had normal or corrected-to-normal eyesight, and gave their informed consent according to the procedures approved by the Dartmouth Committee for the Protection of Human Subjects.

Task design

Trial sequence and timing are shown in Fig. 1. Stimuli were controlled and displayed using Presentation software (http://nbs.neuro-bs.com). The objects came from a canonical set of line drawings (Snodgrass and Vanderwart, 1980), with 50 different objects in each of the two object categories (tools and non-tools). Based on ratings provided in Snodgrass and Vanderwart (1980), tools and non-tools were equated for familiarity (3.6 vs. 3.6, respectively, on a scale of 5) and complexity (2.5 vs. 2.6). On each trial objects were randomly drawn from their category with replacement, with all trials having one tool and one non-tool. Post-experiment debriefing confirmed that all participants remained naïve as to the distinction in object categories. The objects were no larger than approximately 1.5° in either the vertical and/or horizontal dimension (depending on object type), and were presented approximately 2.5° to center from fixation, with the bottom of each object resting on the horizontal meridian. Each participant performed a total of five trial blocks, with each block corresponding to one functional run during fMRI scanning. Blocks began and ended with 20 s of fixation-only “rest” and had a total of 84 trials, equally divided among the four combinations of attend left and attend right (for the cueing condition) and tool-left and tool-right (for the tool location condition). Randomly interspersed with the trials were 27 fixation-only intervals lasting one, two, or three TRs in duration; these intervals were included in order to optimize deconvolution of the event-related hemodynamic response (e.g., Miezin et al., 2000).

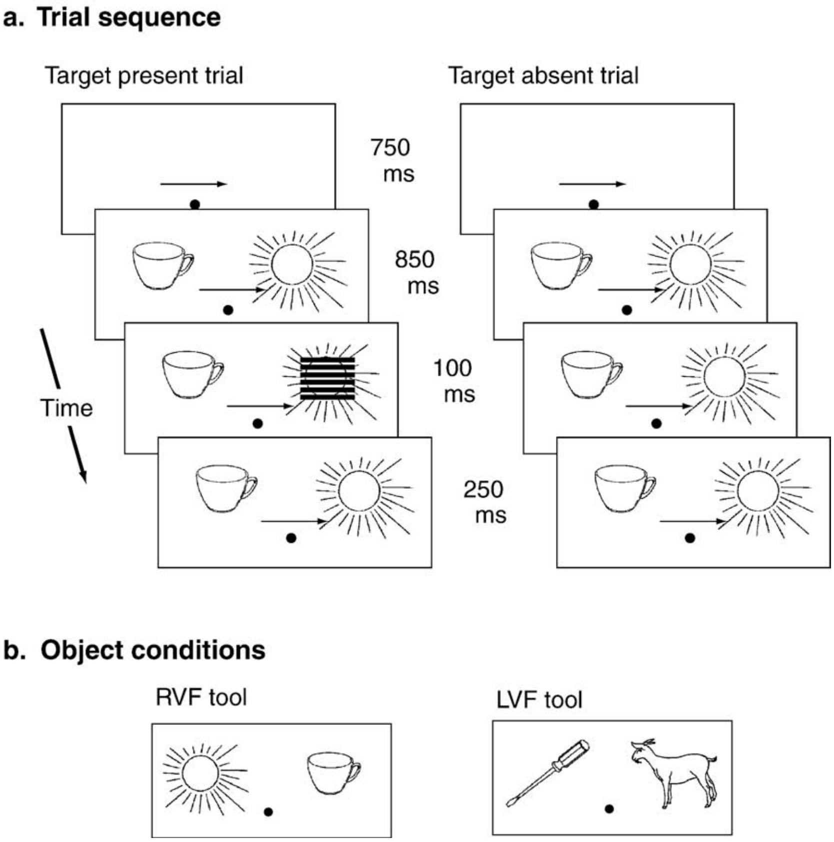

Fig. 1. Trial sequence and conditions. (a) Order and timing of stimuli on each trial. Analysis of fMRI data was restricted to target absent trials. (b) The two object conditions, indicating the location of the tool in the display.

The task required discriminating the spatial frequency of a square-wave grating stimulus that had either a lower (~3 cycles/degree) or higher (~4 cycles/degree) spatial frequency. However, targets were presented on only 20 of the 84 trials, in order to restrict fMRI analysis to trials that contained only objects in the display and that therefore engendered no manual response. Further, to reduce the number of manual responses made by participants, a go/no-go design was used that required a response to be made (with the thumb) only when the target matched a pre-specified spatial frequency (low or high, counterbalanced between participants, as was hand/thumb of response). Because our goal was to maximize attentional orienting to the cued location, the spatial cue always predicted the correct target location. Although this meant that comparisons could not be made between the reaction times to attended versus unattended targets, prior behavioral and event-related potential (ERP) evidence has demonstrated that attention is more optimally focused on the cued location under 100% predictive cueing, relative to conditions that include a small percentage of targets at uncued locations (Handy and Mangun, 2000). Nevertheless, in addition to the fMRI analyses reported below, we also examined the fMRI data for evidence indicating that attention was in fact oriented in response to the spatial cues.[1] In order to confirm that fixation was maintained throughout each trial, eye movements were monitored during scanning using a sclaral reflectance system (Applied Sciences Laboratories Model 504, Bedford, MA). Five participants (2 female, 3 male) were excluded from data analysis due to large (>1°) and frequent eye movements during scanning. Reported results are for the remaining 16 participants.

fMRI recording and analysis

fMRI data were collected using a 1.5-T SIGNA scanner (GE Medical Systems, Milwaukee, WI) with a fast gradient system for echo-planar imaging (EPI). Dense foam padding was used for head stabilization. Scanning was performed in a dimly-lit room, with the visual stimuli rear-projected to a screen behind the participant's head and viewed via a headcoil-mounted mirror. EPI images in-plane with the AC-PC line were acquired using a gradient-echo pulse sequence and sequential slice acquisition (TR = 2500 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 TRs during which no data were acquired to allow for steady-state tissue magnetization. The beginning of each trial and fixation-only interval was synchronized to the onset of acquisition for each EPI volume. A total of 172 EPI volumes were collected in each functional run, and a total of five functional runs were performed by each participant. High-resolution, T1-weighted axial images were also taken of each participant (TR = 25 ms, TE = 6 ms, band width = 15.6 kHz, voxel size = 0.9375 × 1.25 × 1.2 mm). Data were processed and analyzed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). For each subject the EPI images were corrected for motion (Friston et al., 1996) and then spatially-normalized into MNI stereotaxic coordinates using the EPI template provided with SPM99 (Friston et al., 1995a). The normalized EPI images were then spatially smoothed using an isotropic 8 mm Gaussian kernel.

The smoothed, normalized single-subject EPI data were analyzed via multiple regression using the general linear model (Friston et al., 1995b). In particular, the event-related responses to the onset of the bilateral object displays were examined, with the model including regressors for (1) each trial type without targets (as effects of interest) and (2) each trial type with targets (as effects of non-interest). Regressors were based on the canonical event-related hemodynamic response function, temporal derivatives of the event-related responses were included as additional regressors, and low-frequency scanner and/or physiological noise was modeled via linear, quadratic, and cubic regressors of non-interest. Group-level analyses were based on a random-effects model using one-sample t tests. Following this random-effects analysis, mean β values for each participant for the effects of interest, averaged across all voxels within each significant cluster identified in the group-wise data, were extracted from the SPM99 data files using custom scripts implemented in MATLAB (The MATHWORKS Inc., Natick, MA). Time series data for these same clusters were derived using ROI Toolbox as implemented in SPM99 (http://spm-toolbox.sourceforge.net/documentation.html). The time series themselves were computed using selective averaging with condition as the filter. All reported voxel coordinates were converted to Talairach coordinates (Talairach and Tournoux, 1988) using a modified version of the mni2tal MATLAB script (www.harvard.edu/~slotnick/scripts.htm).

Results

Behavior

Analysis of manual responses to the targets indicated that independent of the VF of the target, overall discrimination performance was better with a tool relative to a non-tool in the target location. For reaction times (RTs), this was manifest as a significant main effect of object ($F(1,15) = 5.94$; $P < 0.05$), with RTs faster when a tool was in the attended location, relative to a non-tool (941 ms vs. 976 ms in LVF, 934 vs. 957 in RVF). There was no main effect of visual field ($F(1,15) = 1.04$) or tool by VF interaction ($F(1,15) = 1.24$). For accuracy, there was also a significant main effect of object ($F(1,15) = 7.27$; $P < 0.05$), with the correct response rate higher when a tool was in the attended location relative to a non-tool (0.986 vs. 0.966 in LVF, 0.993 vs. 0.989 in RVF). Again, there was no main effect of VF ($F(1,15) = 0.01$) or tool by VF interaction ($F(1,15) = 0.65$). These results thus

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[1] The volitional orienting of visual spatial attention is associated with the activation of a bilateral parietal–prefrontal network comprising the superior parietal lobule (SPL) and dorsolateral prefrontal cortex (DLPFC) (e.g., Corbetta and Shulman, 2002; Giesbrecht et al., 2003; Hopfinger et al., 2000; Kastner et al., 1998). This predicted that our spatial cues should have activated a similar network. In addition to the fMRI analysis reported in Results, we thus applied a second general linear model to our fMRI data that specifically examined the event-related responses to the onset of the spatial cues as a function of the location cued. Both LVF and RVF cues elicited an increased fMRI BOLD response in bilateral SPL and DLPFC, a pattern not only consistent with the top-down orienting of visual spatial attention, but one that differed from the network of areas typically associated with VMRs, including IPL, PMd, PMv, prePMd, SMA, and preSMA (e.g., Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2002; Grèzes et al., 2003; Handy et al., 2003; Jeannerod, 2001; Picard and Strick, 2001). Further, this analysis also suggests that the effects reported in the text were not simply due to residual overlapping responses from the attention-directing cues that preceded the onsets of the object displays.

suggest that independent of the VF involved, having a graspable object in the attended location had a facilitatory effect on response performance.

fMRI

Because our study was designed to characterize how visual attention modulates implicit VMRs, fMRI data analysis was anatomically restricted a priori to those voxel clusters occurring in regions previously linked to visuomotor functions: the perimotor/premotor area (e.g., Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2002; Grèzes et al., 2003; Handy et al., 2003; Jeannerod, 2001), and adjacent parietal and prefrontal regions (Battaglia-Mayer et al., 2003; Burnod et al., 1999; Caminiti et al., 1998; Marconi et al., 2001; Matelli and Luppino, 2001). Towards identifying relevant voxel clusters of interest, the data were treated as a 2 × 2 design, with factors of tool location (LVF vs. RVF) and whether or not the tool's location was covertly attended (attended vs. unattended). Initial fMRI analysis thus consisted of a set of three contrast pairs in order to identify voxel clusters in the anatomical region of interest (ROI) showing: (1) a main effect of tool location, (2) a main effect of attention state, and/or (3) their interaction—that is, a difference in attention effects between the visual fields. Importantly, this approach of holding the tool location constant and varying whether or not attention was oriented to the tool's location parallels the conventions adopted in electrophysiological studies of spatial attention, where analyses are based on holding stimulus conditions constant and varying the attentional state in order to ascribe effects on stimulus processing to an influence of the latter, rather than a change in the former (see, e.g., Mangun, 1995; Mangun and Hillyard, 1995). These contrasts also held constant any residual overlapping responses from the cues. For any significant voxel clusters found in our ROI in the aforementioned contrast pairs, we then wanted to characterize the nature of the response in each cluster across all four conditions of interest. In this manner, cluster-specific statistical analyses would be used as the means of verifying the response profile idiosyncratic to each voxel cluster, rather than simply interpreting the response profile based on the results of the initial statistical maps. All contrasts reported below are based on a random-effects model and reported at $P < 0.001$ (uncorrected), with a minimum spatial extent (k) of 5 contiguous voxels. Voxel coordinates are given in the stereotaxic coordinates of Talairach and Tournoux (1988).

Main effects contrasts

For main effects of tool location, no significant voxel clusters were found in the ROI that had a significantly larger fMRI blood oxygen-level-dependent (BOLD) response when the tool was in the LVF display location, relative to the RVF (Fig. 2a, left). In contrast, two voxel clusters in our ROI were found showing a significantly larger BOLD response when a tool was in the RVF display location, relative to the LVF (Fig. 2a, right)—left prePMd and left superior parietal lobule (SPL). Cluster coordinates and statistics are reported in Table 1 (top). For main effects of attention, no significant voxel clusters were found in our ROI that had a significantly larger BOLD response when the tool's location in the display was attended relative to unattended (Fig 2b, left), or unattended relative to attended (Fig. 2b, right).

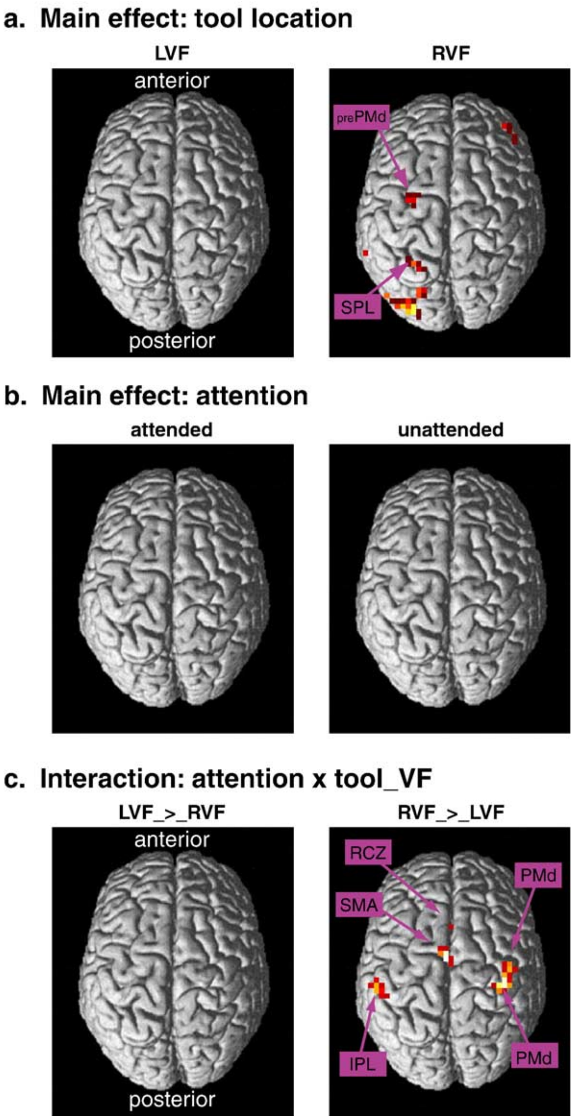

Fig. 2. Main effect and interaction contrasts. (a) Collapsing across attention conditions, no voxel clusters in the brain showed an increased BOLD response specific for a tool in the LVF (left), while two voxels in our anatomical area of interest showed an increased BOLD response specific for a tool in the RVF (right). (b) Collapsing across the visual field involved, no voxel clusters showed a significant increase in the BOLD response for an attended relative to unattended tool, or visa versa. (c) Examining effects unique to attending to a tool in the LVF vs. effects unique to attending to a tool in the RVF—no significant voxel clusters were found that had a larger BOLD response for an attended vs. unattended tool in the LVF, relative to an attended vs. unattended tool in the RVF (left). However, five significant voxel clusters were found that had a larger BOLD response for an attended vs. unattended tool in the RVF, relative to an attended vs. unattended tool in the LVF (right). All contrasts are reported at $P < 0.001$ (uncorrected) and a minimum cluster size of 5 contiguous voxels.

Interaction contrasts

Examining the interaction between the tool's location in the display and the effect of attending to that specific location–that is, effects unique to attending to a tool in the LVF vs. effects unique to attending to a tool in the RVF–no significant voxel clusters were found in the ROI that had a larger BOLD response for an attended

Table 1
Voxel cluster statistics

Figure	Cluster	Talairach coordinates			*t*	*k*	Anatomical locus	
							BA	Gyrus
Fig. 2a/Fig. 3	prePMd	−28	−5	63	4.77	9	6	L Superior Frontal
	L SPL	−28	−52	54	5.34	10	7	L SPL
Fig. 2c/Fig. 4	RCZ	−4	9	33	4.68	10	24	Anterior Cingulate
	SMA	−4	−5	48	5.64	17	6	Medial Frontal
	L IPL	−51	−29	46	5.10	10	40	L Supramarginal
	R PMd	44	−13	45	4.77	12	4	R Pre-Central
	R PMd	40	−20	56	4.89	18	4	R Pre-Central

Reported coordinates and *t* values are for the cluster maxima. *k* = number of voxels in the cluster. BA = Brodmann's area, L = left, R = right, IPL = inferior parietal lobule, SPL = superior parietal lobule, RCZ = rostral cingulate zone, SMA = supplementary motor area.

vs. unattended tool in the LVF, relative to an attended vs. unattended tool in the RVF (Fig. 2c, left). However, five significant voxel clusters were found in the ROI that had a larger BOLD response for an attended vs. unattended tool in the RVF, relative to an attended vs. unattended tool in the LVF (Fig. 2c, right). These included significant clusters in the rostral cingulate zone (or RCZ; see Picard and Strick, 2001), SMA, left IPL, and right PMd. Coordinates and statistics for these clusters are reported in Table 1 (bottom).

Cluster response profiles

Results reported in this section are summarized in Table 2. The response profiles for the two clusters showing a main effect of tool location–left prePMd and left SPL–are presented in Fig. 3. The bar graphs plot the mean response (or mean β, averaged across participants) within each cluster as a function of the tool's location (LVF or RVF) and whether or not that location was attended. As can be seen, both clusters show overall larger responses with the tool in the RVF location of the display. This pattern was confirmed within each cluster via a repeated-measures ANOVA performed on the mean responses, with factors of tool location (LVF vs. RVF) and attention (tool's location attended vs. unattended). For left prePMd, there was a main effect of tool location ($F(1,15) = 22.36$; $P < 0.0005$). For left SPL, there was a main effect of tool location ($F(1,15) = 22.85$; $P < .0005$), as well as an interaction between the tool's location × attention ($F(1,15) = 4.56$; $P < 0.05$). However, when the effect of attention was examined independently within each visual field in left SPL via one-sample *t* tests, the attention effect was not significant in either the LVF ($t(15) = 1.38$) or RVF ($t(15) = 2.57$). While these results indicated that these two voxel clusters were manifesting a differential sensitivity to the visual field location of the tool in the display, there was no reliable effect of attention on the responses that were observed in these clusters.

In contrast, for the five clusters identified via the interaction contrasts (Fig. 2c), the response profiles in Fig. 4 show patterns suggesting that activity within each cluster was not simply covarying with the visual field location of the tool. Instead, each response profile was consistent with an increased response for an attended relative to unattended tool in the RVF, and a decreased response for an attended relative to unattended tool in the LVF. To confirm this pattern, we performed within each cluster a repeated-measures ANOVA on the mean responses within each cluster (or mean βs, averaged across participants) that had factors of attended location (LVF vs. RVF) and the object in that location (tool vs. non-tool). In all 5 clusters, a significant main effect of attention was observed: RCZ ($F(1,15) = 22.45$; $P < 0.0005$), SMA ($F(1,15) = 34.02$; $P < 0.0001$), left IPL ($F(1,15) = 32.22$; $P < 0.0001$), the more inferior cluster in PMd ($F(1,15) = 21.97$; $P < 0.0005$), and the more superior cluster in PMd ($F(1,15) = 24.69$; $P < 0.0005$). Importantly, however, interactions between the attended location and the object in that location were also observed for SMA ($F(1,15) = 6.98$; $P < 0.05$) and left IPL ($F(1,15) = 5.67$; $P < 0.05$). When the effect of attention was examined independently within each visual field for SMA via one-sample t tests, the attention effect reached significance in both the LVF ($t(15) = 7.01$; $P < 0.05$) and RVF ($t(15) = 16.81$; $P < 0.005$). For left IPL, the attention effect also reached significance in both the LVF ($t(15) = 6.07$; $P < 0.05$) and RVF ($t(15) = 4.77$; $P < 0.05$). Taken together, these results indicate that while clusters in the RCZ and right PMd had responses dominated by the location of attention within the visual field, the responses in SMA and left IPL showed a sensitivity to the interaction between the location of attention and the object in the attended location such that there was an increase in the BOLD response for tools in the attended RVF and a decreased BOLD response for tools in the attended LVF.

Table 2
Cluster response profiles

Figure	Cluster	Response profile
Fig. 2a/Fig. 3	prePMd	tool location
	L SPL	tool location
Fig. 2c/Fig. 4	RCZ	attended location
	SMA	attended × tool location
	L IPL	attended × tool location
	R PMd	attended location
	R PMd	attended location

Note: "Response Profile" is based on significance of statistics performed on mean response across attention and tool conditions within each cluster, as reported in Results. Voxel statistics and maxima coordinates are also reported in Results. L = left, R = right, IPL = inferior parietal lobule, SPL = superior parietal lobule, RCZ = rostral cingulate zone, SMA = supplementary motor area.

Discussion

Our study was designed to examine whether voluntary spatial attention can facilitate the implicit VMRs that occur in dorsal

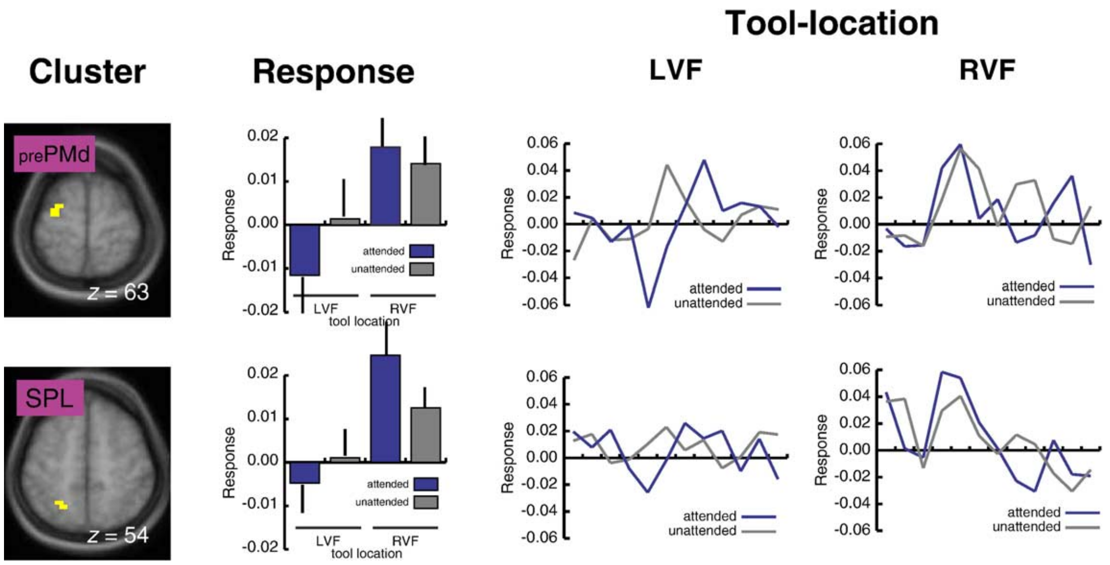

Fig. 3. fMRI BOLD response profiles for clusters identified via a main effect of tool location. These are the clusters identified in Fig. 2a (right), and each cluster is presented on a group-averaged T1-weighted anatomical image. The bar graphs show the magnitude of the response within each cluster (± standard error), as a function of the tool location and whether that location was attended. On the right are shown the time-series data from which response magnitudes were estimated. Statistics performed on the magnitude of response across conditions within each cluster revealed a main effect of tool location in both left prePMd and left SPL. The time series data are plotted at 2.5 s intervals, beginning 5 s prior to stimulus onset.

cortex when a graspable object comes into view. In this regard we report two main findings. First, the fMRI BOLD response in two visuomotor-related areas–SMA and left IPL–showed an interaction between the location of attention and the location of the tool in the bilateral display. That is, the response profiles in these two areas were uniquely determined by the combination of the attended visual field and whether a tool was in that location, and further, were statistically dissociable from those regions in cortex showing activity modulated only by the tool location or only by the attended location. Second, this interaction in SMA and left IPL took the form of a positive BOLD response for tools in the attended RVF and a negative BOLD response for tools in the attended LVF. In other words, not only did attending to the location of the tool modulate the nature of the visuomotor response generated in SMA and left IPL, but the effect took the form of a bidirectional BOLD response that varied with the visual field involved. Given these findings, a number of critical issues follow.

Consequences of spatial selection

First, how do the current results expand our understanding of voluntary attentional orienting and the role it plays in visual processing? The effects of attending non-foveally within the visual field have long been tied primarily–if not exclusively–to influences on visual perception. For example, attention improves signal detection performance (e.g., Bashinski and Bacharach, 1980; Downing, 1998; Handy et al., 1996), increases visual sensory gain (e.g., Heinze et al., 1994; Hillyard et al., 1999), and amplifies stimulus-evoked activity in object perception areas of the ventral visual processing stream (e.g., Wojciulik et al., 1998). Yet, as we discuss below, what our data indicate is that attention may also have consequences for the implicit planning of object-directed actions—actions which are often performed in the absence of directly foveating the object in question. Hands are shaken while maintaining eye contact, coffee cups are grabbed while reading the newspaper, and doors are opened without looking down at the knobs or handles. Indeed, given that in the real world overt perceptual goals typically involve foveating an object of interest rather than covertly attending to it, our results are not inconsistent with the view that the perceptual benefits of spatial attention may be a secondary consequence of a mechanism that evolved primarily to facilitate premotor planning (e.g., Rizzolatti et al., 1987, 1994).

Beyond demonstrating that spatial attention can influence VMRs, the current findings also reveal a notable interaction between attention and automatic processes in cortex. In particular, the VMRs examined here can be considered implicit, in that visuomotor cortex is automatically responding to the presence of a tool in the visual field even though the observer is not consciously aware of either this distinction in object category or of its special significance to the action system (e.g., Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2002; Grèzes et al., 2003; Handy et al., 2003; Jeannerod, 2001). Nevertheless, what our data show is that the network of cortical areas generating these implicit VMRs will vary as a function of whether or not the tool is in a spatial location consciously attended by the observer. This effect cannot be considered an overt influence of attention on visuomotor processes–such as when one is knowingly attending to a planned motor movement (e.g., Rushworth et al., 2001a,b, 1997)–because participants oriented their attention to a spatial location in our paradigm, not a planned motor movement or the motor-related properties of the object in the attended location. Rather, the data suggest that the extent of implicit activity in visuomotor cortex is gated by a spatial selection process occurring at an earlier stage in the afferent visual processing stream, most likely in the extrastriate V4 region (see e.g., Heinze et al., 1994; Woldorff et al., 1997). The implication is that spatial orienting may be a way of biasing object-specific selection in the motor system, with an object in a selected location generating a greater degree of implicit visuomotor analysis in comparison to an object falling within an unattended region of space.

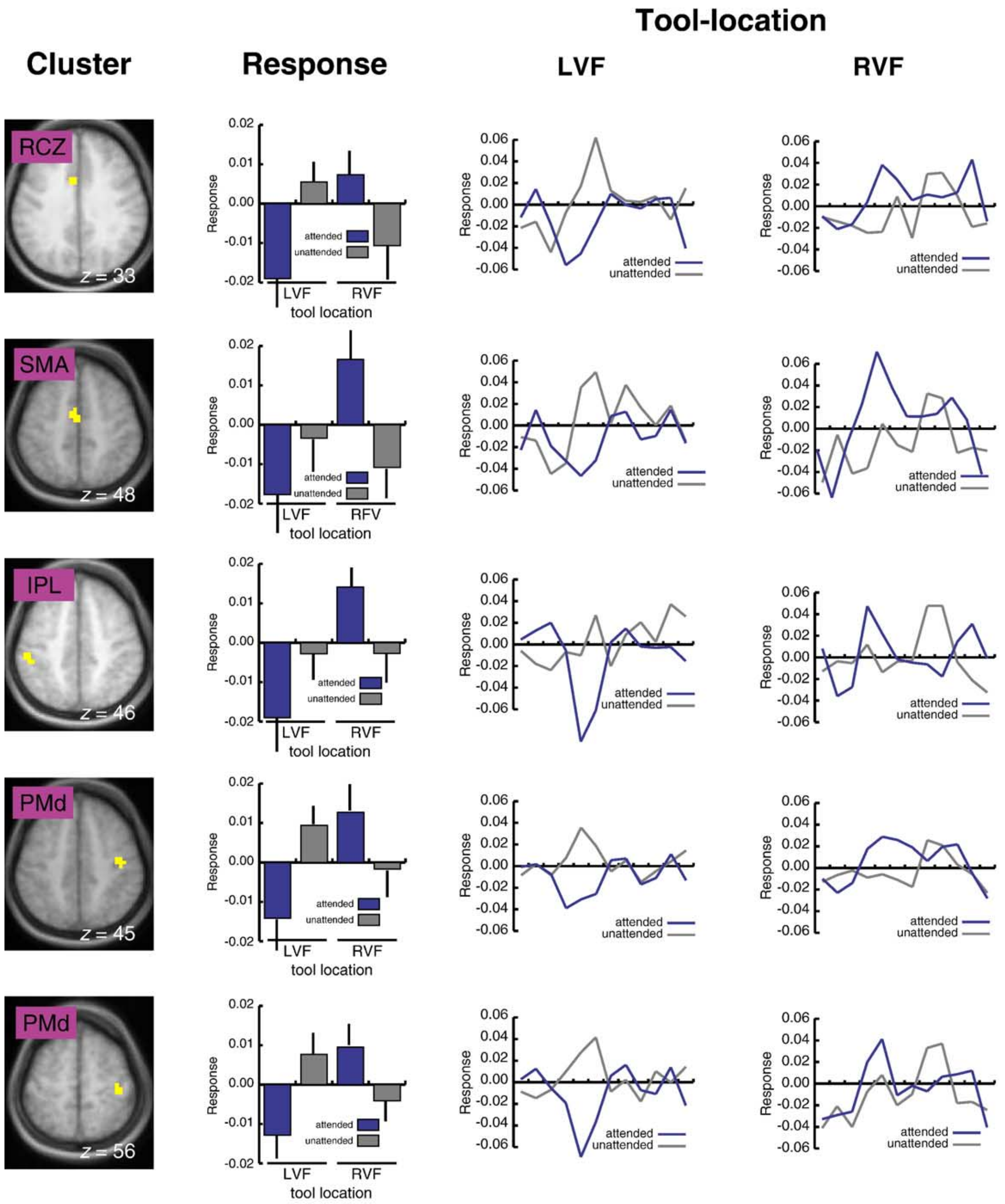

Fig. 4. fMRI BOLD response profiles for clusters identified via the interaction contrast. These are the clusters shown in Fig. 2c (right), and each cluster is presented on a group-averaged T1-weighted anatomical image. The bar graphs show the magnitude of the response within each cluster (± standard error), as a function of the tool location and whether that location was attended. On the right are shown the time-series data from which response magnitudes were estimated. Statistics performed on the magnitude of response across conditions within each cluster revealed that all five clusters showed a main effect of attention. However, only SMA and left IPL also showed a significant interaction between the tool location and attended location. The time series data are plotted at 2.5 s intervals, beginning 5 s prior to stimulus onset.

Importantly, the proposal that spatial orienting can influence what object the motor system selects for possible grasping can also account for how VMRs appear to vary with how attention is deployed within the visual field. To the point, here we found that selectively attending to the location of a tool in the RVF led to an increased fMRI response in left IPL and SMA, yet previously we reported that when the same object display was observed under divided attention conditions, an increased fMRI response was observed in bilateral IPL and bilateral prePMd (Handy et al., 2003). Given that the object display conditions remained constant between studies but the attention conditions varied, what this suggests is that the implicit processing of action-related objects will change with selective versus divided attention. For example, the divided attention conditions used by Handy et al. (2003) are consistent with a situation where the motor system may implicitly recognize that one of the objects within the visual field has a motor affordance, but the motor system has not necessarily engaged in the more selective processes of planning the motor movements idiosyncratic to that object. Instead, that level of implicit motor planning may only begin to occur (in the current paradigm, at least) when visual attention is exclusively oriented to the object's location and all other objects in the display fall out of the zone of attentional focus.

If spatial attention can be viewed as modulating implicit VMRs in this manner, how might the effect be described at a more specified level? One answer lies in considering the functions of the particular cortical regions involved. Activation of IPL has been associated with both paying attention to planned motor actions (e.g., Rushworth et al., 1997, 2001a,b) and sensorimotor processing in general (e.g., Mattingley et al., 1998), whereas SMA has been tied to the organization, awareness, and perceptual control of movement (e.g., Haggard and Magno, 2001; Haggard and Whitford, 2004). Moreover, both IPL and SMA–along with preSMA and PMd–have been shown to activate more strongly when imagining versus actually executing a reaching movement (e.g., Gerardin et al., 2000). Such data are consistent with the proposal that voluntary spatial attention may serve to facilitate the implicit planning of object-directed actions. However, our prior findings showed that under conditions where spatial attention was not voluntarily oriented to a specific spatial location, left IPL showed a similar pattern to that observed here–a positive BOLD response for tools in the RVF location of the display and a negative BOLD response for tools in the LVF location–while no effects of any kind were found in SMA (Handy et al., 2003). This raises the possibility that the modulatory influence of voluntary spatial attention in the visuomotor domain can be more narrowly characterized as gating the functions of SMA—functions associated with higher-level aspects of visuomotor planning (e.g., Haggard and Magno, 2001; Haggard and Whitford, 2004).

Although visuomotor activity in SMA may uniquely depend on voluntary spatial selection, the functional properties of left IPL also warrant consideration. To the point, the left anterior supramarginal gyrus of the IPL has consistently shown activation when a task involves paying attention to planned motor actions (Rushworth et al., 1997, 2001a,b; see also Rowe et al., 2002). Based on the idea that "motor attention" involves the updating of body and limb representations to current motor-related goals, what this has suggested is that left IPL may be responsible for generating these updated representations when a graspable object is first analyzed in visuomotor cortex (e.g., Rushworth et al., 2003). If this hypothesis is valid, the activation of left IPL by tools in the RVF in both the current experiment and in our previous study (Handy et al., 2003) would support the possibility that the updating of motor representation can occur even in the absence of conscious motor attention. Indeed, that motor updating may not require conscious intent is certainly an idea consistent with the experiences of everyday life, wherein objects are frequently grasped with little if any attention applied to the planning and execution of the movements involved. Nevertheless, given that IPL comprises a broader region of the parietal lobe than just the anterior supramarginal gyrus linked to explicit motor attention, the possibility that a common region of left IPL is involved in both motor attention and implicit VMRs remains to be directly tested.

Negative BOLD response

Another issue to consider is whether the negative BOLD response (NBR) identified for tools in the attended LVF should be considered as functionally significant. One view is that it should not be, a position positing that the modulatory effects of spatial attention on visuomotor processing are restricted to the RVF (see also Handy et al., 2003). The alternative view is that the NBR is in fact indicative of a functional consequence for attention-visuomotor interactions in the LVF, but if so, what evidence supports that position? Although an NBR may be due in part to a redistribution of cerebral blood flow in response to non-local neural activity, it appears to include a significant contribution from local decreases in neural activity (e.g., Shmuel et al., 2002; Smith et al., 2004). This indicates that the NBR reported here may in fact reflect changes in neural activation states. At the same time, the NBR was associated with only one of our four experimental conditions, and occurred in voxel clusters identified via a positive BOLD response in at least one of the other three experimental conditions. As a consequence, the NBR was not being generated in a brain region–such as the precuneus and posterior cingulate gyrus–that may show a non-selective decrease in hemodynamic activity in response to the onset of cognitive activity in general (e.g., Raichle, 1999; Shulman et al., 1997). Finally, we could not attribute the NBR to an artifact of a global scaling correction during data analysis, as this data transformation was rightly not included in our fMRI analysis protocols (e.g., Aguirre et al., 1998; Desjardins et al., 2001).

Instead, behavioral performance demonstrated that independent of the visual field involved, manual responses were quicker and more accurate with a tool in the attended location relative to a non-tool. While there is growing recognition that meaningful fMRI patterns will not always correlate with behavioral performance (see Wilkinson and Halligan, 2004), our data show that conditions associated with a NBR in SMA and left IPL were also associated with facilitated behavioral performance. Further, regions of visual cortex have been shown to have a BOLD response that varies in its direction (positive or negative) depending on the visual field location being stimulated (Shmuel et al., 2002) as well as the attentional state of the observer (e.g., Smith et al., 2000; Tootell et al., 1998)—both factors clearly involved in the current data pattern. The available evidence thus makes it difficult to conclusively rule out–at least for now–the possibility that attentional modulation of VMRs for LVF objects may in fact be characterized as manifesting a functionally-significant NBR.

Visual field asymmetries

Regardless of whether to functionally interpret the NBR reported here, given that voluntary spatial attention appears to differentially modulate VMRs as a function of visual field, how should this visual field asymmetry be characterized? One of the hallmarks of spatial attention is that we have a stronger bias to orient to the RVF rather than the LVF, as measured by behavioral performance (e.g., Mangun et al., 1994; Reuter-Lorenz et al., 1990). Yet the behavioral data in the current study showed no such RVF bias. Instead, it was the fMRI data showing a pattern consistent with visual field asymmetries, and in particular, asymmetries in the VMR as a function of the visual field location of the tool in the display. What this suggests is that there may be a dissociation in the underlying processes indexed by the behavioral and fMRI measures in our paradigm. For example, whether or not a visual illusion influences behavioral performance appears to depend on both the locus of that illusion in visual processing and the nature of the task being performed; if an illusion arises from processing in the visuoperceptual pathway, then the illusion will be manifest in behavior when performing a visuoperceptual task, but not when performing visuomotor task (Dyde and Milner, 2002; Milner and Dyde, 2003). Following similar logic here, if the fMRI data were reflecting visuomotor processes while behavioral performance depended on processes idiosyncratic to the visuoperceptual pathway, it could account for why a visual field asymmetry was observed in the former but not the latter—the behavioral task did not depend on engaging the visuomotor processes which were uniquely manifesting the asymmetry.

While the foregoing may help explain why behavioral performance failed to show the visual field asymmetry observed in the fMRI data, left unexplained is why visuomotor processing should manifest the asymmetry in the first place. That is, why might visuomotor cortex show a greater response for action-related objects in the RVF relative to the LVF? Towards understanding this question, much evidence has suggested that the representation and planning of motor movements may be lateralized to the left cerebral hemisphere (e.g., Bradshaw, 2001; Haaland and Harrington, 1996; Rushworth et al., 2001a,b; Schluter et al., 2001). As a result, this may produce a RVF bias in action-related processing when viewing natural scenes containing objects in both visual hemifields—under these conditions, the objects within each lateral hemifield are preferentially processed by the contralateral cerebral hemisphere (e.g., Boles, 1983, 1994). In other words, the RVF bias in the VMR may be driven by a left hemisphere dominance for visuomotor processing—a possibility certainly congruent with the involvement of left but not right IPL in the current data pattern.

Conclusions

The overarching issue raised by our study is that in a brain showing dissociable visual pathways for perception and action (e.g., Milner and Goodale, 1995; Mishkin et al., 1983), spatial attention appears to have the capacity to modulate activity not just in the visuoperceptual pathway (see Handy et al., 2001), but in the visuomotor pathway as well. As such, a final question to consider is whether attention-related modulations of visuomotor processing in the dorsal "action" stream occur directly or are mediated via attentional effects arising in the ventral "perception" stream. In this regard, action-related processes can operate on visual object representations that are independent of representations associated with canonical visual perception (e.g., Ganel and Goodale, 2003; Hodges et al., 1999). Further, in the corticocortical projections extending beyond the V2/V3/V4 complex in occipital cortex, the input into posterior parietal cortex is dominated by information originating in parafoveal retinotopic locations, whereas the input into the inferior temporal cortex is dominated by information originating in the fovea (e.g., Baizer et al., 1991; Morel and Bullier, 1990). Given that spatial attention can modulate sensory processing at a locus within visual cortex–the V4 region (e.g., Heinze et al., 1994; Woldorff et al., 1997)–that is prior to the bifurcation into the dual processing streams, it would appear that the neurophysiology is in place to allow a direct influence of spatial attention on processing in the dorsal/action pathway. Yet at the same time, the priming of semantic information by object recognition processes in the ventral/perception pathway has been shown to include activation of premotor cortex when the object in question is associated with grasping (e.g., Martin et al., 1995, 1996). Indeed, given that significant cross-talk certainly exists between the dorsal and ventral processing streams (e.g., Milner and Goodale, 1995; Seki, 1993; Van Essen and DeYoe, 1995), it would not be surprising to find that attention can exert an influence on visuomotor processing via both direct and indirect routes. What our data here suggest is that we should now be asking exactly these questions.

References

Aguirre, G.K., Zarahn, E., D'Esposito, M., 1998. The inferential impact of global signal covariates in functional neuroimaging analyses. NeuroImage 8, 302–306.

Baizer, J.S., Ungerleider, L.G., Desimone, R., 1991. Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. J. Neurosci. 11, 168–190.

Bashinski, H.S., Bacharach, V.R., 1980. Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. Percept. Psychophys. 28, 241–248.

Battaglia-Mayer, A., Caminiti, R., Lacquaniti, F., Zago, M., 2003. Multiple levels of representation of reaching in the parieto-frontal network. Cereb. Cortex 13, 1009–1022.

Boles, D.B., 1983. Hemispheric interaction in visual field asymmetry. Cortex 19, 99–113.

Boles, D.B., 1994. An experimental comparison of stimulus type, display type, and input variable contributions to visual field asymmetry. Brain Cogn. 24, 184–197.

Bonfiglioli, C., Duncan, J., Rorden, C., Kennett, S., 2002. Action and perception: evidence against converging selection processes. Vis. Cogn. 9, 458–476.

Bradshaw, J.L., 2001. Asymmetries in preparation for action. Trends Cogn. Sci. 5, 184–185.

Burnod, Y., Baraduc, P., Battaglia-Mayer, A., Guigon, E., Koechlin, E., Ferraina, S., Lacquaniti, F., Caminiti, R., 1999. Parieto-frontal coding of reaching: an integrated framework. Exp. Brain Res. 129, 325–346.

Caminiti, R., Ferraina, S., Battaglia Mayer, A., 1998. Visuomotor transformations: early cortical mechanisms of reaching. Curr. Opin. Neurobiol. 8, 753–761.

Chao, L.L., Martin, A., 2000. Representation of manipulable man-made objects in the dorsal stream. NeuroImage 12, 478–484.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev., Neurosci. 3, 201–215.

Craighero, L., Fadiga, L., Rizzolatti, G., Umiltà, C., 1999. Action for perception: a motor-visual attentional effect. J. Exp. Psychol. Hum. Percept. Perform. 25, 1673–1692.

Desjardins, A.E., Kiehl, K.A., Liddle, P.F., 2001. Removal of confounding effects of global signal in functional MRI analyses. NeuroImage 13, 751–758.

Deubel, H., Schneider, W.X., Paprotta, I., 1998. Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. Vis. Cogn. 5, 81–107.

Downing, C.J., 1998. Expectancy and visuo-spatial attention: effects on perceptual quality. J. Exp. Psychol. Hum. Percept. Perform. 13, 228–241.

Dyde, R.T., Milner, A.D., 2002. Two illusions of perceived orientation: one fools all of the people some of the time; the other fools all of the people all of the time. Exp. Brain Res. 144, 518–527.

Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.-P., Heather, J.D., Frackowiak, R.S.J., 1995a. Spatial registration and normalization of images. Hum. Brain Mapp. 2, 165–189.

Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.-P., Frith, C.D., Frackowiak, R.S.J., 1995b. Statistical parametric maps in functional imaging: a general linear approach. Hum. Brain Mapp. 2, 189–210.

Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S., Turner, R., 1996. Movement-related effects in fMRI time-series. Magn. Reson. Med. 35, 346–355.

Ganel, T., Goodale, M.A., 2003. Visual control of action but not perception requires analytical processing of object shape. Nature 426, 664–667.

Gerardin, E., et al., 2000. Partially overlapping neural networks for real and imagined hand movements. Cereb. Cortex 10, 1093–1104.

Giesbrecht, B., Woldorff, M.G., Song, A.W., Mangun, G.R., 2003. Neural mechanisms of top-down control during spatial and feature attention. NeuroImage 19, 496–512.

Grafton, S.T., Fadiga, L., Arbib, M.A., Rizzolatti, G., 1997. Premotor cortex activation during observation and naming of familiar tools. NeuroImage 6, 231–236.

Grèzes, J., Decety, J., 2002. Does visual perception of object afford action? Evidence from a neuroimaging study. Neuropsychologia 40, 212–222.

Grèzes, J., Tucker, M., Armony, J., Ellis, R., Passingham, R.E., 2003. Objects automatically potentiate action: an fMRI study of implicit processing. Eur. J. Neurosci. 17, 2735–2740.

Haaland, K.Y., Harrington, D.L., 1996. Hemispheric asymmetry of movement. Curr. Opin. Neurobiol. 6, 796–800.

Haggard, P., Magno, E., 2001. Localising awareness of action with transcranial magnetic stimulation. Exp. Brain Res. 127, 102–107.

Haggard, P., Whitford, B., 2004. Supplementary motor area provides an efferent signal for sensory suppression. Cogn. Brain Res. 19, 52–58.

Handy, T.C., Mangun, G.R., 2000. Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. Percept. Psychophys. 62, 175–186.

Handy, T.C., Kingstone, A., Mangun, G.R., 1996. Spatial distribution of visual attention: perceptual sensitivity and response latency. Percept. Psychophys. 58, 613–627.

Handy, T.C., Hopfinger, J.B., Mangun, G.R., 2001. Functional neuroimaging of attention processes. In: Cabeza, R., Kingstone, A. (Eds.), Handbook on Functional Neuroimaging of Cognition. MIT Press, Cambridge, MA, pp. 75–108.

Handy, T.C., Grafton, S.T., Shroff, N.M., Ketay, S., Gazzaniga, M.S., 2003. Graspable object grab attention when the potential for action is recognized. Nat. Neurosci. 6, 421–427.

Heinze, H.J., et al., 1994. Combined spatial and temporal imaging of brain activity during visual selective attention in humans. Nature 372, 543–546.

Hillyard, S.A., Vogel, E.K., Luck, S.J., 1999. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. In: Humphreys, G.W., Duncan, J., Treisman, A. (Eds.), Attention, Space, and Action: Studies in Cognitive Neuroscience. Oxford, New York, pp. 31–53.

Hodges, J.R., Spatt, J., Patterson, K., 1999. "What" and "how": evidence for the dissociation of object knowledge and mechanical problem-solving skills in the human brain. Proc. Natl. Acad. Sci. U. S. A. 96, 9444–9448.

Hopfinger, J.B., Buonocore, M.H., Mangun, G.R., 2000. The neural mechanisms of top-down attentional control. Nat. Neurosci. 3, 284–291.

Humphreys, G.W., Riddoch, M.J., 2001. Detection by action: neuropsychological evidence for action-defined templates in search. Nat. Neurosci. 4, 84–88.

Jeannerod, M., 2001. Neural simulation of action: a unifying mechanism for motor cognition. NeuroImage 14, S103–S109.

Kastner, S., De Weerd, P., Desimone, R., Ungerleider, L.G., 1998. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. Science 282, 108–111.

Mangun, G.R., 1995. Neural mechanisms of visual selective attention. Psychophysiology 32, 4–18.

Mangun, G.R., Hillyard, S.A., 1995. Mechanisms and models of selective attention. In: Rugg, M.D., Coles, M.G.H. (Eds.), Electrophysiology of Mind: Event-Related Brain Potentials and Cognition. Oxford, New York, pp. 40–85.

Mangun, G.R., Luck, S.J., Plager, R., Loftus, W., Hillyard, S.A., Handy, T.C., Clark, V.P., Gazzaniga, M.S., 1994. Monitoring the visual world: hemispheric asymmetries and subcortical processes in attention. J. Cogn. Neurosci. 6, 267–275.

Marconi, B., et al., 2001. Eye-hand coordination during reaching: I. Anatomical relationships between parietal and frontal cortex. Cereb. Cortex 11, 513–527.

Martin, A., Haxby, J.V., Lalonde, F.M., Wiggs, C.L., Ungerleider, L.G., 1995. Discrete cortical regions associated with knowledge of color and knowledge of action. Science 270, 102–105.

Martin, A., Wiggs, C.L., Ungerleider, L.G., Haxby, J.V., 1996. Neural correlates of category-specific knowledge. Nature 379, 649–652.

Matelli, M., Luppino, G., 2001. Parietofrontal circuits for action and space perception in the macaque monkey. NeuroImage 14, S27–S32.

Mattingley, J.B., Husain, M., Rorden, C., Kennard, C., Driver, J., 1998. Motor role of human inferior parietal lobe revealed in unilateral neglect patients. Nature 392, 179–182.

Miezin, F.M., Maccotta, L., Ollinger, J.M., Petersen, S.E., Buckner, R.L., 2000. Characterizing the hemodynamic response: effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. NeuroImage 11, 735–759.

Milner, A.D., Dyde, R.T., 2003. Why do some perceptual illusions affect visually guided action, when others don't? Trends Cogn. Sci. 7, 10–11.

Milner, A.D., Goodale, M.A., 1995. The Visual Brain in Action. Oxford, New York.

Mishkin, M., Ungerleider, L.G., Macko, K.A., 1983. Object vision and spatial vision: two cortical pathways. Trends Neurosci. 6, 414–417.

Morel, A., Bullier, J., 1990. Anatomical segregation of two cortical visual pathways in the macaque monkey. Vis. Neurosci. 4, 555–578.

Pavese, A., Buxbaum, L.J., 2002. Action matters: the role of action plans and object affordances in selection for action. Vis. Cogn. 9, 559–590.

Picard, N., Strick, P.L., 2001. Imaging premotor areas. Curr. Opin. Neurobiol. 11, 663–672.

Raichle, M.E., 1999. The neural correlates of consciousness: an analysis of cognitive skill learning. In: Gazzaniga, M.S. (Ed.), The New Cognitive Neurosciences. MIT Press, Cambridge, MA, pp. 1305–1318.

Reuter-Lorenz, P.A., Kinsbourne, M., Moscovitch, M., 1990. Hemispheric control of spatial attention. Brain Cogn. 12, 240–266.

Riddoch, M.J., Humphreys, G.W., Edwards, S., Baker, T., Willson, K., 2003. Seeing the action: neuropsychological evidence for action-based effects on object selection. Nat. Neurosci. 6, 82–89.

Rizzolatti, G., Riggio, L., Dascola, I., Umiltá, C., 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. Neuropsychologia 25, 31–40.

Rizzolatti, G., Riggio, L., Sheliga, B.M., 1994. Space and selective attention. In: Umilta, C., Moscovitch, M. (Eds.), Attention and Performance, vol. XV. MIT Press, Cambridge, MA, pp. 231–265.

Rowe, J., Friston, K., Frackowiak, R., Passingham, R., 2002. Attention to action: specific modulation of corticocortical interactions in humans. NeuroImage 17, 988–998.

Rushworth, M.F.S., Nixon, P.D., Renowden, S., Wade, D.T., Passingham, R.E., 1997. The left parietal cortex and motor attention. Neuropsychologia 35, 1261–1273.

Rushworth, M.F.S., Krams, M., Passingham, R.E., 2001a. 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.

Rushworth, M.F.S., Ellison, A., Walsh, V., 2001b. Complementary localization and lateralization of orienting and motor attention. Nat. Neurosci. 4, 656–661.

Rushworth, M.F.S., Johansen-Berg, H., Göbel, S.M., Devlin, J.T., 2003. The left parietal and premotor cortices: motor attention and selection. NeuroImage 20, S89–S100.

Schluter, N.D., Krams, M., Rushworth, M.F.S., Passingham, R.E., 2001. Cerebral dominance for action in the human brain: the selection of actions. Neuropsychologia 39, 105–113.

Seki, S., 1993. A Vision of the Brain. Blackwell, Boston.

Shmuel, A., Yacoub, E., Pfeuffer, J., Van de Moortele, P.-F., Adriany, G., Hu, X., Ugurbil, K., 2002. Sustained negative BOLD, blood flow and oxygen consumption response and its coupling to the positive response in the human brain. Neuron, 36, 1195–1210.

Shulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R., Miezin, F.M., Raichle, M.E., Petersen, S.E., 1997. Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. J. Cogn. Neurosci. 9, 648–663.

Smith, A.T., Singh, K.D., Greenlee, M.W., 2000. Attentional suppression of activity in the human visual cortex. NeuroReport 11, 271–277.

Smith, A.T., Williams, A.L., Singh, K.D., 2004. Negative BOLD in the visual cortex: evidence against blood stealing. Hum. Brain Mapp. 21, 213–220.

Snodgrass, J.G., Vanderwart, M., 1980. 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.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme Medical Publishers, New York.

Tipper, S.P., Lortie, C., Baylis, G.C., 1992. Selective reaching: evidence for action-centered attention. J. Exp. Psychol. Hum. Percept. Perform. 18, 891–905.

Tootell, R.B.H., Hadjikhani, N., Hall, E.K., Marrett, S., Vanduffel, W., Vaughan, J.T., Dale, A.M., 1998. The retinotopy of visual spatial attention. Neuron 21, 1409–1422.

Tucker, M., Ellis, R., 1998. On the relations between seen objects and components of potential actions. J. Exp. Psychol. Hum. Percept. Perform. 24, 830–846.

Tucker, M., Ellis, R., 2004. Action priming by briefly presented objects. Acta Psychol. 116, 185–203.

Van Essen, D.C., DeYoe, E.A., 1995. Concurrent processing in the primate visual cortex. In: Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences. MIT, Cambridge, MA, pp. 383–400.

Ward, R., 1999. Interaction between perception and action systems: a model for selective action. In: Humphreys, G.W., Duncan, J., Treisman, A. (Eds.), Attention, Space, and Action: Studies in Cognitive Neuroscience. Oxford University Press, New York, pp. 311–332.

Weir, P.L., Weeks, D.J., Welsh, T.N., Elliott, D., Chua, R., Roy, E.A., Lyons, J., 2003. Influence of terminal action requirements on action-centered distractor effects. Exp. Brain Res. 149, 207–213.

Wilkinson, D., Halligan, P., 2004. The relevance of behavioural measures for functional-imaging studies of cognition. Nat. Rev., Neurosci. 5, 67–73.

Wojciulik, E., Kanwisher, N., Driver, J., 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: an fMRI study. J. Neurophysiol. 79, 1574–1578.

Woldorff, M.G., Fox, P.T., Matzke, M., Lancaster, J.L., Veeraswamy, S., Zamarripa, F., Seabolt, M., Glass, T., Gao, J.H., Martin, C.C., Jerabek, P., 1997. Retinotopic organization of early visual spatial attention effects as revealed by PET and ERPs. Hum. Brain Mapp. 5, 280–286.