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Selective attention modulates inferior frontal gyrus activity during action observation

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Our ability to recognize the actions of others is subserved by a complex network of brain areas, including the inferior frontal gyrus (IFG), inferior parietal lobe (IPL) and superior temporal sulcus (STS). An unresolved issue is whether the activity within these regions requires top-down control or whether it arises relatively automatically during passive action observation. Here we used fMRI to determine whether cortical activity associated with action observation is modulated by the strategic allocation of selective attention. Participants observed moving and stationary images of reach-to-grasp hand actions, while they performed an attentionally demanding task at the fovea. We first defined regions-of-interest (ROIs) in the IFG, IPL and STS which responded to the perception of these actions. We then probed these ROIs while participants observed the identical, but now task-irrelevant, actions and instead performed an easy (low attentional load) or difficult (high attentional load) visual discrimination task. Our data indicate that the activity of the left IFG was consistently attenuated under conditions of high attentional load, while the remaining action observation areas remained relatively unaffected by attentional manipulations. The suppression of the left IFG was unique to the observation of hand actions, and did not occur during the observation of non-biological control stimuli, in the form of coherent dot motion. We propose that the left IFG is the site at which descending inhibitory processes affect the processing of observed actions, and that the attentional modulation of this region is responsible for filtering task-irrelevant actions during ongoing behavior.

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Introduction

The human ability to recognize and interpret the actions of others is fundamental to communication and social perception. It is well established that action observation activates a complex network of brain areas, including the posterior inferior frontal

gyrus (IFG, Brodmann's areas 44/45), the rostral inferior parietal lobe (IPL) and the superior temporal sulcus (STS) (Decety and Grèzes, 1999; Grèzes and Decety, 2001; Rizzolatti et al., 2001). The putative macaque homologues of these areas (ventral premotor area F5, inferior parietal area PF and the STS, respectively) contain cellular units which respond to biological actions, including goal-directed movements of the hand. In particular, a subpopulation of 'mirror neurons' in areas F5 and PF are sensitive to both the observation and the execution of reach-to-grasp hand actions (Gallese et al., 1996; Rizzolatti et al., 2001). Together, the activity of these areas is thought to be involved in the encoding and interpretation of observed gesture (Rizzolatti and Craighero, 2004).

Given the biological and human significance of action recognition, it has been postulated that perceived actions automatically recruit areas within the action observation network (Buccino et al., 2004; Coricelli, 2005; Gallese, 2003; Gallese et al., 1996; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996; Wilson and Knoblich, 2005). Current behavioral data from humans support the hypothesis that perceived actions are processed without the need for top-down control. For example, observing a goal-directed action typically facilitates the execution of the same, relative to a different movement (Brass et al., 2001, 2000; Craighero et al., 2002; Stürmer et al., 2000; Vogt et al., 2003), and may more generally prime movements involving the corresponding body part (Bach et al., 2007). These priming effects occur despite the observed action being task-irrelevant, which suggests that the processing of these actions cannot be suppressed, even if it is detrimental to task performance. Similar results have been found in studies that have recorded motor-evoked potentials (MEPs) from the extremities following transcranial magnetic stimulation (TMS) of primary motor cortex. These studies demonstrate that passively observing a hand movement results in MEPs in the corresponding arm and hand muscles of the participant, even though participants never themselves initiate a hand movement (Fadiga et al., 1995). Together, these results have been taken to suggest that observed actions are processed automatically and without conscious effort (Rizzolatti and Craighero, 2004; Wilson and Knoblich, 2005).

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A hallmark of strongly automatic processes is that they operate without drawing on general cognitive resources, and that they are not subject to voluntary control (Pashler, 1998). If action observation is an automatic process, as implied by numerous behavioral observations, it should be relatively resistant to modulation by top-down mechanisms such as directed attention. This would be analogous to the operation of closely allied neural systems that are involved in the processing of biologically relevant stimuli. For example, amygdala activity in response to threat-related facial expressions persists even when participants' attention is directed toward a distractor stimulus (Vuilleumier et al., 2001; Williams et al., 2004) or is masked from awareness (Whalen et al., 1998). Such findings suggest that neural systems that evolved to extract the meaning and significance of biologically important stimuli, such as facial expressions, can influence behavior without the need for selective attention. Given the social importance of understanding the actions of others, it might be predicted that action observation areas in the brain would also be relatively immune to modulation by selective attention.

Clearly, however, there will be occasions when it is beneficial to suppress the processing of an observed action, especially if it is irrelevant or otherwise distracting. Consider, for example, being engaged in conversation with a colleague at a cocktail party, and having the distracting gestures of another guest fall within your line of sight. Here, selective attention is crucial to enhance the processing of behaviorally relevant stimuli – the sounds and lip movements made by the person to whom one is speaking – and to suppress the processing of the distracting gestures. Indeed, a recent behavioral study found that the visuomotor priming effects described earlier may only occur when the observed actions fall within participants' focus of spatial attention (Bach et al., 2007). This is consistent with the operation of several other perceptual systems, in which attention plays a crucial modulatory role (Lavie, 1995, 2000). For example, neural signals associated with the perception of several classes of visual stimulus, including visual motion, faces and places, are reduced or even eliminated when participants are engaged in a separate task that involves a high attentional load (Pessoa et al., 2002; Schwartz et al., 2005; Yi et al., 2004).

Previous studies of the neural correlates of action observation in humans have used displays without a competing cognitive or perceptual load. Thus, the extent to which the activity within the action observation network is maintained under conditions of inattention is not known. If actions constitute a special class of stimuli with particular biological and social significance, neural activity associated with action observation should be unaffected by manipulations of attentional load. By contrast, if activity within action observation areas is constrained by the same processing bottleneck as other perceptual systems, as suggested by recent behavioral findings, then increasing the attentional load of a secondary task should attenuate this activity. Here we used fMRI to examine whether responses within human action observation areas can be modulated by selective attention during the observation of reach-to-grasp actions.

Materials and methods

Participants

Sixteen right-handed, neurologically normal volunteers were recruited for this study. One participant was excluded based on a

structural abnormality in his MRI scan. The remaining 15 participants (7 females) had an age range of 23–39 years (mean 27.3 years). All participants had normal or corrected-to-normal visual acuity. Volunteers were informed about potential risks and gave informed consent prior to entering the study. This study was approved by the ethics committees of St. Vincent's Health and the University of Melbourne, Australia.

Procedure

Stimuli

We showed images of reach-to-grasp hand actions while participants were engaged in a separate, attentionally demanding task (Fig. 1). Reach-to-grasp movements have been widely used in human studies of perception of action (Tipper, 2004), and have also been shown to engage action observation areas in the IFG, IPL and STS. Specifically, our stimuli comprised images of a hand reaching for a centrally positioned target object (a vertically oriented rod) from the left or right side of the screen, with either a two-fingered grip or a whole-hand grip. Because action observation areas have most likely evolved to recognize naturalistic movements that unfold over time, we presented participants with images of moving hand actions in order to identify only those areas that respond to moving biological stimuli. We then aimed to probe these areas under varying conditions of load during action observation.

Two additional control conditions were included. First, motion can be a powerful exogenous cue that could direct attention to the observed action. Thus, in order to control for the amount of motion present in the stimulus, participants also viewed stationary images of the same actions. Comparing the effect of attentional load between Moving and Stationary Hands allowed us to distinguish the effect of attention on the dynamics of hand movement from its effect on the perception of the action itself (Johnson-Frey et al., 2003). The stationary images depicted the hand just prior to it making contact with the rod, and were single frames extracted from the corresponding movie clips. For both the Moving and Stationary Hands, reaches traversed $\sim 17^\circ$ of visual angle, and displays of left-sided reaches were mirror-reversed images of right-sided reaches.

Second, to ensure that the effect of attention on action observation areas was not a generalized effect independent of the observed stimulus, participants also viewed images of moving non-biological stimuli, in the form of coherent dot motion. These stimuli consisted of 100 dots presented in a 10×10 starting grid over $\sim 17^\circ$ of visual angle. Once the motion commenced, the net direction of movement was either to the left or right of the display. The degree of motion coherence was titrated for each participant according to the method described below. Across participants, the average motion coherence was 66%. Those dots that were moving coherently had a velocity of 47°/s; the remaining dots were distributed randomly.

Superimposed on every hand action was a small, centrally positioned diamond-shaped frame (subtending $\sim 4.5^\circ$ visual angle from corner-to-corner). In the attentional load task, participants were required to discriminate the larger of two gaps that appeared on opposite sides of this diamond frame. The attentional load of this task was systematically manipulated by varying the relative spatial dimensions of the gaps, such that the difference in size between one pair of gaps could be large and therefore easier to discriminate (39-pixel difference; Low Load condition), or small

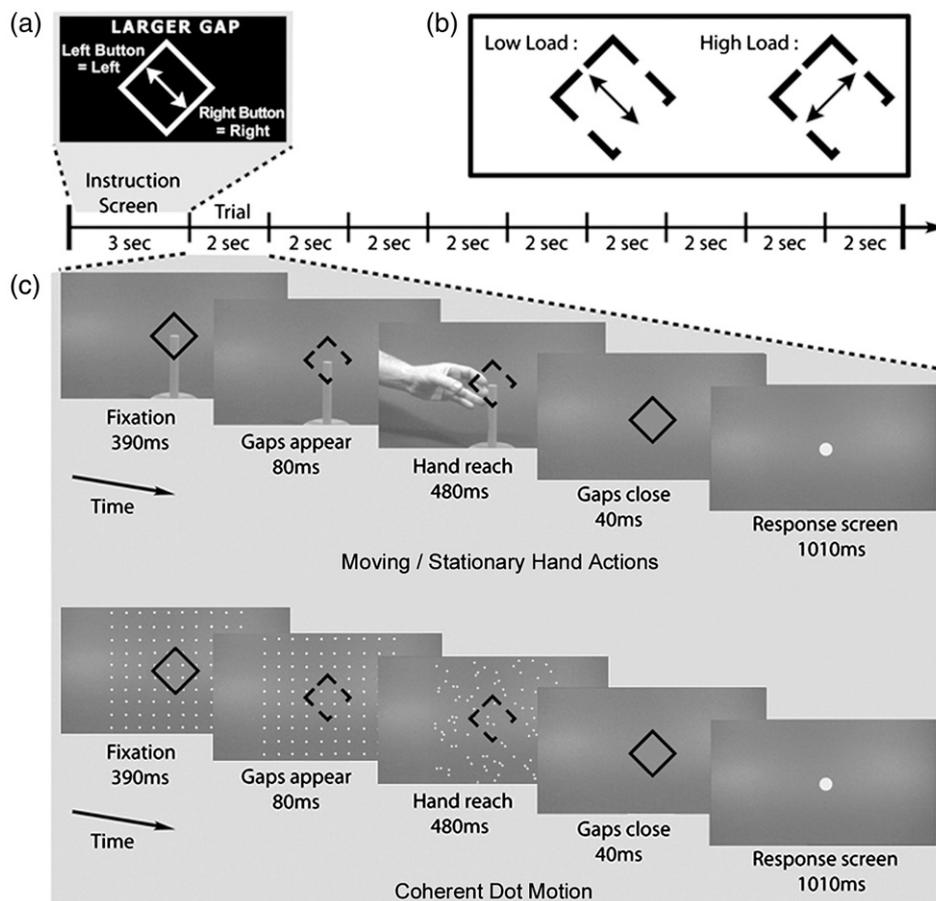


Fig. 1. Time course of a typical trial and block during the attentional load runs. (a) Participants were instructed at the beginning of each block to attend to two opposite sides of a central diamond frame. The task was to judge the relative sizes of gaps that appeared on these two sides. (b) The relative spatial disparity between the opposing gaps could be large (low attentional load) or small (high attentional load). (c) Blocks consisted of nine 2 s trials, during which participants observed a reach-to-grasp hand action or coherent dot motion, on which the diamond frame was superimposed. In the localizer run, participants ignored the frame and attended to the moving hand action to discriminate its grasp (two-finger or whole-hand grasp). In the attentional load runs, participants ignored either the hand action or the dot motion stimuli and attended to the diamond frame to perform the gap discrimination (attentional load) task. Importantly, identical stimuli were presented in both the high- and low-attentional load conditions.

and therefore difficult to discriminate (two-pixel difference; High Load condition). An instruction screen appeared at the beginning of each block of trials, indicating the two sides of the diamond to which participants had to attend.

In each trial, the onset of the hand action or dot motion stimuli occurred 80 ms after the onset of the gaps in the central diamond, and were present for 480 ms for all stimuli (Fig. 1). At the conclusion of the reach or the dot motion, the gaps were filled in for 40 ms, and all stimuli were removed from the display. Participants were then required to make a relevant unsped response by button-press.

Behavioral task

Prior to scanning, we first confirmed the attentionally demanding nature of the gap discrimination task by examining its effect on participants' behavioral responses to the Moving and Stationary Hand actions. Participants were required to perform the gap discrimination (attentional load) task as described above, while simultaneously discriminating the type of grip formed by the observed hand (two-finger versus whole-hand). Responses were unsped and registered by button-press.

The amount of dot motion coherence was initially set at 70%. For each participant, this coherence was titrated in increments of 10% to result in the same performance decrement under High relative to Low Load as that during the observation of Moving and Stationary Hands (approximately 20%).

Importantly, in order to maintain stimulus conditions across the entire experiment, the displays used in the behavioral task were identical to those used in the subsequent fMRI localizer task and attentional load runs. The stimuli were rear-projected with a 1024×768 screen resolution and 60 Hz refresh rate to deliver stimuli of the same visual angle that would be experienced within the scanner. Trials were delivered in six separate counterbalanced blocks comprising High and Low Load trials for Moving Hands, Stationary Hands and Dot Motion. Forty trials were conducted for each of these six conditions. For the hand action stimuli, an equal number of trials involved reaches that were left- or right-sided, and two-fingered or whole-hand grasps. For the dot stimuli, an equal number of trials involved leftward and rightward motion. With regards to the gap discrimination task, the larger gap appeared with equal probability on any of the four sides of the diamond outline. Within each block, the order of trials was randomized.

fMRI localizer task

During the scanning session, each participant completed a localizer run to functionally determine regions-of-interest (ROIs) within known action observation areas. The localizer task required participants to attend to stimuli of Moving Hands and to discriminate their grip type. In the baseline condition, participants observed the central diamond alone and were required to discriminate its color (red or blue), thus making minimal demands on attention. To ensure that participants held their gaze centrally during the localizer and baseline tasks, the displays were designed such that the grip component of the reach-to-grasp action was not revealed until the hand overlapped with the central diamond. Responses were provided with one of two hand-held optic fiber button boxes.

During the localizer run, an instruction screen appeared at the beginning of each block, informing participants of the upcoming task (to discriminate grip type or diamond color). Each trial lasted 2 s, during which participants had 1010 ms following the offset of the stimulus in which to respond. Nine trials were presented in each block, and there were six blocks for each stimulus condition (Moving Hands, Color Discrimination). The order of blocks was pseudo-randomized, and rest blocks were intermingled. Blocks of stationary images were also displayed but are not analyzed here, as our aim in this study was to identify only those action observation areas that responded to moving biological stimuli.

fMRI attentional load task

To explore the effect of attentional load on neural responses within action observation areas, we conducted three further fMRI runs, in which participants viewed stimuli of Moving Hands, Stationary Hands and Dot Motion. During these runs, participants viewed the identical (but now task-irrelevant) stimuli, while performing the attentionally demanding gap discrimination task alone. Prior to each block of trials, an instruction screen informed participants as to which two opposing sides of the central diamond they were to attend (Fig. 1). For each trial, participants had 1010 ms to discriminate the larger gap (in separate blocks of High and Low Load) and provide a response with a left or right button press. The mapping of responses to buttons was matched so that the overall number of left- and right-hand responses would be equivalent across the critical manipulation of attentional load. This ensured that any difference between the level of neural activity for low- and high-load conditions could not be attributed to differences in motor planning, preparation or response selection.

As in the localizer run, nine trials were presented in each block, and there were six blocks for each stimulus condition (High Load and Low Load). The order of blocks was pseudo-randomized, and rest blocks were intermingled. The order in which participants performed the localizer and experimental runs was counter-balanced.

fMRI scan acquisition

Functional MR images were acquired at St. Vincent's Hospital, Melbourne, using a whole-body 1.5-T Siemens MAGNETOM Avanto scanner with a gradient-echo echo-planar imaging (EPI) sequence. The scanner was equipped with a standard radio-frequency birdcage headcoil for signal transmission and reception. Lateral head stabilizers were used to minimize head movement. Scanning was performed in a darkened room, with the visual stimuli rear-projected to a screen that stood at the foot of the gantry of the MRI scanner and viewed via a headcoil-mounted mirror. EPI

images were acquired at a 30° axial oblique plane using a gradient-echo pulse sequence and sequential slice acquisition ($T_R=3000$ ms, $T_E=40$ ms, flip angle=78°, 32 contiguous slices with a slice thickness of 4.0 mm and without an interslice gap, in-plane resolution of 96×128 pixels in a FOV of 220×206 mm). Each functional run began with eight T_R periods, data from which were not analyzed, to allow for steady-state tissue magnetization. A total of 179 EPI volumes were collected for each functional run, and a total of three functional runs were performed by each participant. High-resolution, T2-weighted structural images were also taken of each participant.

fMRI data analyses

Data were processed and analyzed using SPM2 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London; <http://www.fil.ion.ucl.ac.uk/spm> (Friston et al., 1995); implemented in Matlab (Mathworks Inc., USA)). For each subject, the EPI images were realigned to the first image for movement correction by using a least-squares approach and six-parameter rigid body spatial transformations (Friston et al., 1995). These images were then spatially normalized into Montreal Neurological Institute (MNI) stereotaxic coordinates using the EPI template provided with SPM2 (Mazziotta et al., 1995). The normalized EPI images were then spatially smoothed using an isotropic Gaussian kernel at 8 mm full-width at half-maximum (Friston et al., 1995).

The effects of the experimental paradigm were estimated for each participant on a voxel-by-voxel basis using the principles of the general linear model. For the localizer run, the smoothed, normalized single-subject EPI data were analyzed by modeling Moving Hands, Color Discrimination and Rest blocks using boxcar functions convolved with the canonical haemodynamic response function, including a high-pass filter with 128 s cut-off. For the two experimental runs, the High Load, Low Load and Rest blocks were modeled with similar convolved boxcar functions and 128 s high-pass filter. Group analysis was then performed using standard random-effects analysis (Holmes and Friston, 1998).

Given that the IFG, IPL and STS have consistently been implicated in action observation tasks (Decety and Grèzes, 1999; Grèzes and Decety, 2001; Rizzolatti et al., 2001), we used an ROI approach to provide greater sensitivity in detecting differences specifically in these areas under conditions of High versus Low Load. In the localizer run, we conducted a within-subjects analysis of variance (ANOVA) on the contrast of Moving Hands>Rest compared with Color Discrimination (baseline)>Rest to obtain clusters in the IFG, IPL and STS that were most active during the observation of Moving Hands. The statistical threshold was set at $p<0.05$, corrected for multiple comparisons with a false discovery rate (FDR) of 0.05 (Genovese et al., 2002; Nichols and Hayasaka, 2003). Clusters of fewer than four voxels were ignored (Forman et al., 1995). Of the clusters that were significant at a group level, we selected those with peak voxels falling within the IFG, IPL and superior temporal cortex as defined by the Wake Forest University PickAtlas (Maldjian et al., 2003), and defined ROIs as spheres of 10 mm radius around these peak voxels for subsequent analysis of the attentional load conditions (Calvo-Merino et al., 2005; Grèzes et al., 2003).

In the attentional load runs, first-level analyses were conducted for each participant, by performing the contrasts of High Load>Rest and Low Load>Rest for the Moving Hands, Stationary Hands and Dot Motion conditions separately. In a random-effects group analysis, we then used paired *t*-tests to obtain

the critical contrasts of (High Load>Low Load) and (Low Load>High Load). To analyze the effect of attentional load specifically within the action observation network, we masked these comparisons with the functional ROIs derived from the localizer runs. We considered as significant those voxels that survived a correction for multiple comparisons with a family-wise error rate (FWE) of $p < 0.05$. Anatomical details of significant signal changes were obtained by superimposing the SPM maps on the high-resolution T1 canonical MNI template image provided in SPM2.

Results

Behavioral performance

Behavioral data verified the efficacy of the gap discrimination task in limiting participants' capacity to attend to the observed actions. A repeated measures ANOVA was conducted on participants' gap discrimination accuracy, with factors of Load (High vs. Low) and Session (Preliminary Session vs. Scanning Session). As expected, this analysis demonstrated that participants were less accurate in discriminating gap size in the High Load relative to the Low Load condition [$F(1,14)=149.152$, $p < 0.001$]. Notably, the ANOVA confirmed that performances in the Preliminary and Scanning Sessions were not significantly different [Load \times Session interaction, $F(1,14)=1.682$, $p = 0.216$; Fig. 2].

Crucially, participants were significantly poorer at discriminating the background stimulus (hand action or coherent dot motion) when they concurrently performed the High Load relative to the Low Load gap discrimination task. This was the case for all three stimulus types: Moving Hands (78.0% vs. 96.8%, $t(14)=8.143$, $p < 0.001$), Stationary Hands (77.7% vs. 99.5%, $t(14)=10.168$, $p < 0.001$), and Coherent Dot Motion (57.3% vs. 80.7%, $t(14)=11.003$, $p < 0.001$). These behavioral data confirm that the High Load task significantly reduced participants' ability to focus their attention on the task-irrelevant hand or dot motion stimuli.

Imaging data

Whole-brain analysis: effect of high attentional load

Before considering the critical issue of whether attentional load modulates neural responses in action observation areas, we first performed a whole-brain analysis to verify that the gap discrimination task yielded measurable changes in BOLD responses in areas of the brain associated with the control of selective attention. It is well established that tasks that involve attentional orienting recruit a network of right-lateralized frontoparietal areas (Corbetta and Shulman, 2002; Kanwisher and Wojciulik, 2000). We therefore performed an initial whole-brain analysis, contrasting the BOLD responses for the High Load versus Low Load conditions for Moving and Stationary Hands. At an uncorrected threshold of $p < 0.001$, this comparison revealed widespread activity in the superior and inferior parietal lobule, the intraparietal sulcus, inferior and middle frontal gyri, and frontal eye fields. Other areas that were more strongly engaged during the High Load task included the insula, anterior cingulate, cuneus and precuneus (see Supplementary Fig. 1). Although increases in activity were found bilaterally, they were more prominent in the right than in the left hemisphere, consistent with previous findings of a right-lateralized attention network.

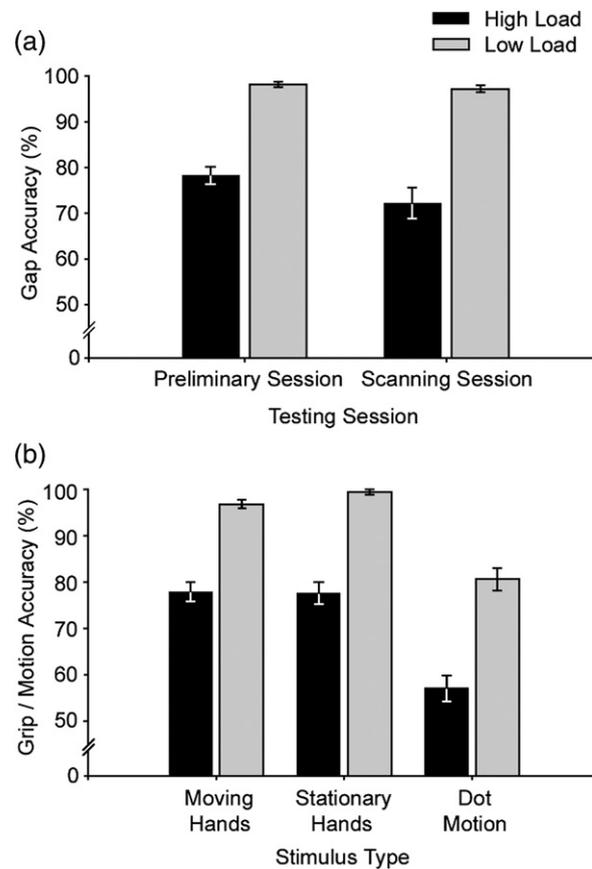


Fig. 2. Results of participants' behavioral performance in the action observation task. (a) Accuracy (mean % correct \pm 1 SEM) as a function of attentional load in the high and low attentional load conditions, which involved discriminating the relative sizes of gaps on a central diamond. Results are from behavioral data acquired prior to and during scanning. (b) Accuracy (mean % correct \pm 1 SEM) in the grip discrimination and motion discrimination tasks under conditions of high- and low-attentional load. Data are plotted separately for the observation of Moving Hands, Stationary Hands and Dot Motion.

Localization of action observation areas

In the localizer run, participants were required to attend to the hand stimuli and discriminate the type of grip formed by the observed hand. Relative to baseline, the observation of Moving Hands resulted in bilateral activation within the pars triangularis of the IFG, corresponding to BA 45 (left $t=3.56$, $p_{FDR}=0.027$; right $t=3.68$, $p_{FDR}=0.022$; Fig. 3; see Supplementary Table 1). In addition to this IFG activity, clusters were also found in the rostral IPL bilaterally (left $t=6.23$, $p_{FDR}=0.002$; right $t=5.34$, $p_{FDR}=0.002$) and in the right supramarginal gyrus (SMG; $t=3.47$, $p_{FDR}=0.032$). Strong bilateral activation was also found within the STS (left $t=6.76$, $p_{FDR}=0.002$; right $t=5.83$, $p_{FDR}=0.002$). This is consistent with existing neuroimaging data that have identified the IFG, IPL and STS as important components in the action observation network (Rizzolatti and Craighero, 2004).

Effect of attentional load on action observation areas

Having verified that the gap discrimination task significantly influenced participants' perception of reach-to-grasp actions, as well as neural activity within the attentional network, we then

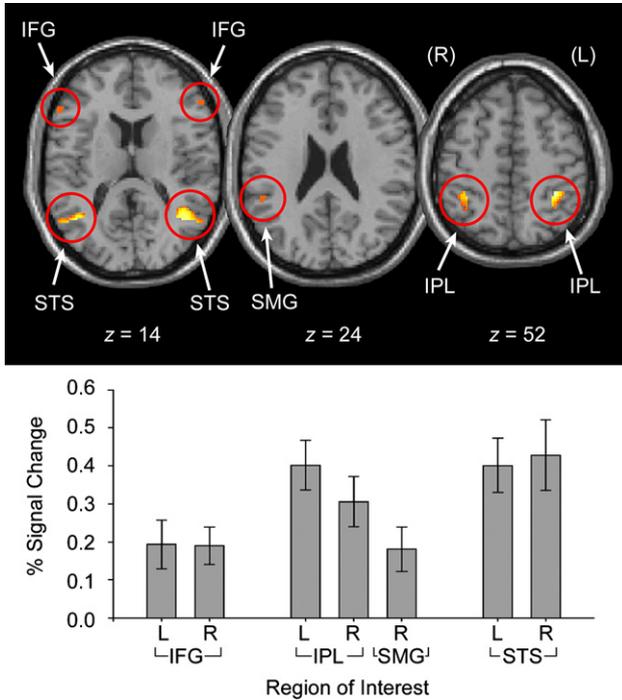


Fig. 3. Results from the localizer task used to identify action observation areas. The top panel shows active clusters within the IFG, IPL and STS that responded to the observation of Moving Hands. All clusters survived correction for multiple comparisons with a false discovery rate of 0.05. Images are shown on axial sections in radiological convention. The lower panel shows the signal change within each region-of-interest relative to baseline. IFG, inferior frontal gyrus; IPL, inferior parietal lobe; SMG, supramarginal gyrus; STS, superior temporal sulcus.

tested for any difference in BOLD signal between the conditions of Low Load and High Load within the functionally defined ROIs (Fig. 4a).

The critical contrast involved comparing activity in the Low Load relative to the High Load condition. If the attentional load of a secondary task at the fovea attenuates neural responses to observed actions, then activity within action observation regions should be reduced in the High Load compared with the Low Load condition. For Moving Hands, a single cluster in the left IFG (pars triangularis; BA 45) demonstrated precisely this pattern of activation, and was significantly *less active* under conditions of High Load relative to Low Load ($t=5.44$, $p_{FWE}=0.006$; Fig. 4b; see Supplementary Table 2). A similar pattern was found during the observation of Stationary Hands, during which significant

reductions in signal intensity were found over two clusters within the left IFG ($t=4.87$, $p_{FWE}=0.025$; $t=4.78$, $p_{FWE}=0.027$; Fig. 4c; see Supplementary Table 2). These findings are illustrated in Figs.

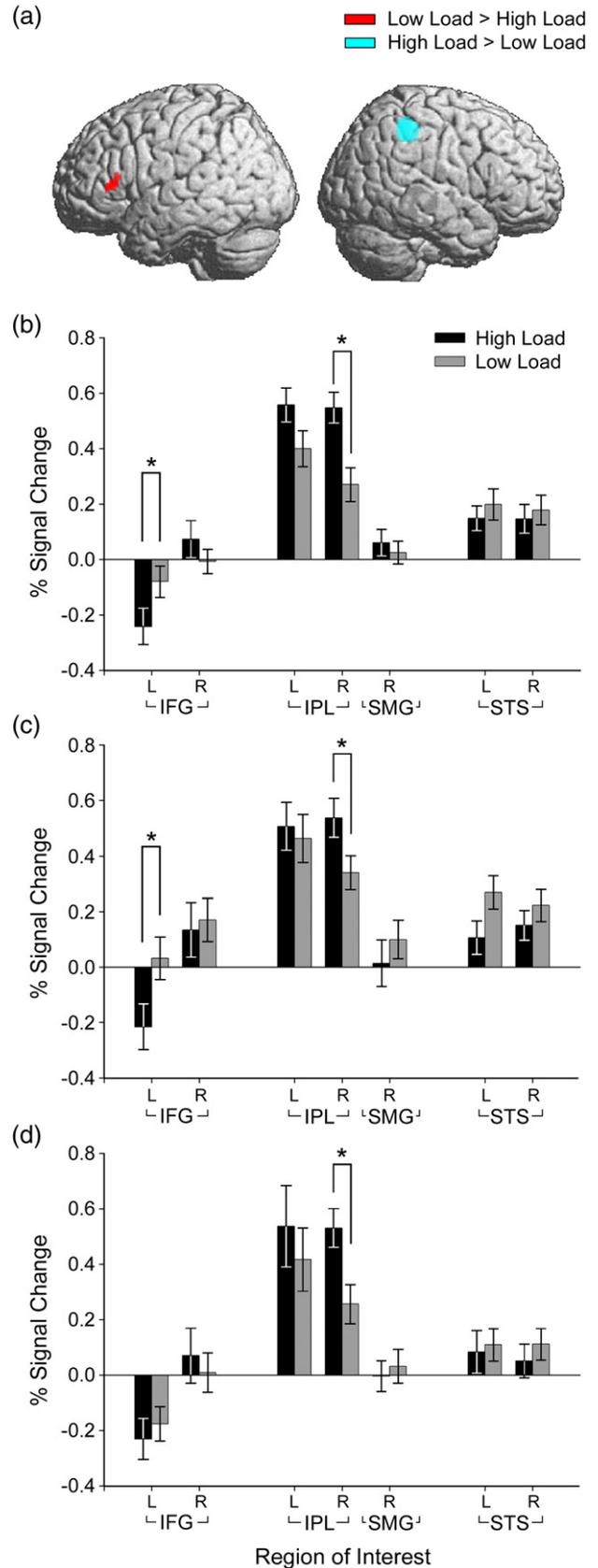


Fig. 4. Results from the attentional load task. (a) Rendered view of the lateral surface of the hemispheres, illustrating clusters of greater activity in the Low Load>High Load contrast (red) and in the High Load>Low Load contrast (blue) during the observation of Moving Hands. For illustrative purposes, clusters are shown at an uncorrected threshold of $p=0.001$. (b, c, d) Graphs illustrate ROI responses in the high- and low-attentional load conditions during the observation of (b) Moving Hands, (c) Stationary Hands, and (d) Dot Motion. The ordinate represents the percent signal change (± 1 SEM) across spheres of 10 mm radius centered on the peak voxels determined in the functional localizer. *Significant difference between mean signal intensity in the High and Low Load conditions, after correction for multiple comparisons ($p_{FWE}<0.05$). Abbreviations as in Fig. 3.

4b and c as a reduction in mean signal intensity across the entire region-of-interest in the left IFG. Crucially, however, this attenuation of signal from the left IFG was not seen during the observation of Dot Motion (Fig. 4d). In fact, in the Dot Motion condition, the only areas that were suppressed under high relative to low load were located outside the ROIs examined, predominantly in the occipital cortex, temporo-occipital junction, middle temporal gyrus, and the middle and superior frontal gyri (see Supplementary Table 3). Taken together, these findings indicate that the suppression of activity in the left IFG under conditions of high attentional load occurs only during the observation of biological actions, and regardless of the amount of explicit motion present in the action stimulus.

In a final analysis the reverse contrast was performed, comparing the effect of High Load relative to Low Load within each ROI. Across all classes of stimuli (i.e., Moving Hands, Stationary Hands and Dot Motion), there were clusters within the right IPL that were more active under High Load relative to Low Load [Moving $t=6.19$, $p_{FWE}=0.001$; $t=6.07$, $p_{FWE}=0.002$ (Fig. 4b); Stationary $t=5.24$, $p_{FWE}=0.040$ (Fig. 4c); Dot Motion $t=5.71$, $p_{FWE}=0.003$ (Fig. 4d)]. These clusters overlap with those revealed in the whole-brain analysis that compared the effect of load on attentional networks, and the consistent attentional effect on this area for all three classes of stimulus suggests that it may play a more general role in cognitively demanding tasks. Indeed, previous studies have shown that these areas are activated by tasks involving attentional load (Culham et al., 2001), visual working memory (Courtney et al., 1997), memory load (Cohen et al., 1997), and cognitive set shifting (Konishi et al., 1998). Notably, there was no increased activity within the left hemisphere for this contrast for any of the three stimulus types.

Discussion

Our results demonstrate that the neural encoding of observed actions can be modulated by the intentional allocation of selective attention. Specifically, we found that activity within the left pars triangularis (BA 45) is reduced by having observers engage in an attentionally demanding task at the fovea. This effect manifested as a relative decrease in activity in this sector under conditions of High Load relative to Low Load. Critically, this difference in activity cannot be attributed to low-level feature differences between the High and Low Load tasks, as identical stimuli were used for both conditions. Moreover, the greater activity in the Low Load relative to the High Load condition cannot simply reflect a generalized increase in neural activity across the ROIs examined, as this effect was specific to the left pars triangularis. In addition, this suppression could not be due to a generalized effect of attention within the pars triangularis, because it was unique to the observation of moving and stationary hand actions, and did not occur in the presence of non-biological stimuli. This contrasts with the increased activity in the right IPL under conditions of High Load, which occurred for all three classes of stimulus, and is thus more likely to reflect its involvement in more general processing during cognitively demanding processes (Cohen et al., 1997; Corbetta and Shulman, 2002; Courtney et al., 1997; Culham et al., 2001; Konishi et al., 1998).

The data presented here advance a recent behavioral finding that task-irrelevant gestures may only result in involuntary visuomotor priming if they appear at an attended spatial location (Bach et al., 2007). This finding by Bach and colleagues (2007)

highlights the importance of spatial attention in the processing of observed gesture. However, in the present study, the attentional load task appeared at the same spatial locus as the observed actions (at fixation), yet attention continued to modulate both behavioral performance and neural activity. Thus, our data further emphasize the importance of selective processes during action observation. In this regard, the sensitivity of the left IFG to the attenuating effects of attention is similar to findings in other neural systems. For example, areas involved in the perception of visual motion, faces and places are known to be sensitive to manipulations of attentional load (Pessoa et al., 2002; Schwartz et al., 2005; Yi et al., 2004). Here the attentional susceptibility of the IFG could reflect its role in gating the processing of task-irrelevant gestures. In everyday life, we are frequently confronted with situations in which several gestures or actions are observed simultaneously (e.g., during group social interactions). One might therefore anticipate the existence of a mechanism that prevents unnecessary processing of actions that are not immediately relevant.

Our findings also converge with those of a recent fMRI study that reported a similar variation in left frontal responses, but as a function of task instruction rather than attentional load (Iacoboni et al., 2005). In this previous study, the authors argued that areas that are activated automatically should not be differentially susceptible to strategic demands (e.g., observing an action with no explicit purpose vs. observing with the purpose of understanding the action). Although the right IFG did appear to operate independent of participants' observational strategy, the authors also found that the left frontal cortex was differentially active, depending on whether participants were passively observing an action or actively inferring the actor's intent. Thus, although the experimental approach and motivation of this earlier study differed significantly from those of the present experiment, both sets of data indicate a unique susceptibility of the left IFG to top-down modulation – either by observational strategy (Iacoboni et al., 2005) or selective attention (as presented here).

Given the putative homologies between Broca's area (BA 44/45) and macaque area F5 (Fadiga et al., 1995; Matelli et al., 1985; Rizzolatti and Arbib, 1998), an important issue to address is to what extent the attentional suppression of the left pars triangularis may be driven by mirror neuron activity. Cytoarchitectonic evidence suggests that Broca's area is a homologue of ventral premotor area F5, in which mirror neurons were first discovered (Matelli et al., 1985; Von Bonin and Bailey, 1947). Within Broca's area itself, some authors have suggested that BA 44, as opposed to BA 45, may more closely resemble macaque area F5 (Geyer et al., 2000; Petrides and Pandya, 1994). Furthermore, human mirror areas are generally defined as those that respond to the observation, execution and imitation of gesture (Iacoboni et al., 1999). However, the re-analysis of a large fMRI data set in humans found that the pars triangularis is involved only in the perception of simple intransitive finger movements, and not during the imitation of those movements (Molnar-Szakacs et al., 2005). This contrasts with the dorsal sector of the pars opercularis (BA 44), which was engaged during both action observation and imitation, and is therefore the more likely homologue of mirror area F5.

Although the issue of IFG homology has not been conclusively resolved, the above considerations suggest that one must be cautious in attributing the attenuation of the left pars triangularis in this experiment to modulation at the level of mirror neurons. This is especially because this experiment involved only passive action observation, and did not require participants to perform any

complex motor responses (such a similar or dissimilar reach-to-grasp action). An important task for future human studies would be to verify whether attention continues to play an important role when participants are required to perform a concurrent motor task. It would also be most useful for future studies on non-human primates to examine the effect of attentional manipulations on individual mirror neurons, in order to directly link the present findings to responses at the cellular level.

The involvement of the pars triangularis in action observation, but not imitation, has led some authors to postulate its involvement in inhibiting the automatic imitation of observed actions (Molnar-Szakacs et al., 2005). By this account, the pars triangularis acts as a node through which the action observation network is subject to top-down control. Our findings provide further evidence in favor of this suggestion by demonstrating its marked sensitivity to the influence of selective attention. Notably, despite being significantly active in the localizer task, the signal change in the left pars triangularis was reduced to levels at, or slightly below, baseline even under conditions of low attentional load (Figs. 4b and c). This result indicates that the mere presence of a secondary task – even one that is relatively undemanding – is sufficient to suppress activity in this region.

The susceptibility of the pars triangularis to top-down control is consistent with anatomical connectivity data, which show that BA 45 receives extensive afferent connections from the orbital and dorsolateral regions of the prefrontal cortex, in contrast with BA 44 which receives connections predominantly from motor, somatosensory and inferior parietal areas (Deacon, 1992; Petrides and Pandya, 2002). The orbital and dorsolateral prefrontal cortices are thought to be important sources of inhibitory control, as evidenced by neuropsychological data indicating that lesions to these areas can lead to pathological imitation of the actions and goals of others (Cummings, 1993; De Renzi et al., 1996; Lhermitte et al., 1986). The connections of BA 45 with these other areas of prefrontal cortex therefore suggest that the ‘release’ phenomena such as echopraxia and imitation behavior (Lhermitte et al., 1986; Luria, 1966) may reflect a loss of inhibitory control over the pars triangularis (cf. Berthier et al., 2006).

Taken together, our findings imply that voluntary attention can exert an attenuating influence on the action observation network, but that this effect is not ubiquitous. In fact, the activity within action observation areas outside the left IFG were not altered by our experimentally induced increase in attentional load. These responses are similar to those found in other perceptual systems (e.g., the amygdala), whose responses to biological stimuli remain unaltered under conditions of high attentional load, visual masking and perceptual suppression (Vuilleumier et al., 2001; Whalen et al., 1998; Williams et al., 2004). Indeed, the pattern of activity within the remaining action observation areas follows that predicted by previous suggestions that these areas encode observed actions automatically (Buccino et al., 2004; Coricelli, 2005; Gallese, 2003; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996; Wilson and Knoblich, 2005). The relative immunity of these areas to attention may therefore represent the neural instantiation of behavioral findings that actions observed in the absence of a secondary task can be processed regardless of their task relevance (Brass et al., 2001; Brass et al., 2000; Craighero et al., 2002; Stürmer et al., 2000; Vogt et al., 2003). In particular, the automatic activation of these areas may underlie the reaction time costs when participants perform actions that are incongruent with those they observe (Brass et al., 2000; Craighero et al., 2002).

It is worth noting that the nature of the secondary task used in our study required participants to perform a visual discrimination while observing task-irrelevant actions. Altering the visual discriminability of a stimulus is one of several methods adopted in previous studies to manipulate selective attention (Mattingley et al., 2006). Other examples include increasing the number of items in a display or increasing the complexity of the required judgment (Lavie, 1995, 2000). The advantage of our paradigm is that we manipulated the attentional load of the task, while maintaining an identical stimulus display across conditions of high and low load. Nevertheless, any task that has the effect of modulating the degree of stimulus processing under varying conditions of load should result in differential competition for limited processing resources, and thus differential processing of task-irrelevant stimuli (Lavie, 2005). Thus, although we chose to modulate attentional load by altering visual discriminability, we would expect a similar pattern of results for other manipulations of load, provided all other task-related factors were adequately controlled.

A particular feature of our study was the use of stationary images to control for the effects of attention on the dynamics of observed hand actions. Previous neuroimaging studies have found that motion-sensitive areas of visual cortex (i.e., the V5/MT complex) are susceptible to the effects of attention, such that their activity is reduced under conditions of high versus low load (Schwartz et al., 2005). It might be suggested that our finding of significantly reduced activity in the left IFG during the observation of moving hands arose merely as a downstream manifestation of attentional modulation of early motion-sensitive areas. However, we found the same effect of attention on left pars triangularis activity for the *stationary* reach-to-grasp actions, which did not involve an explicit motion signal. We can thus rule out any explanation of our findings for the left pars triangularis in terms of attentional modulation of motion-sensitive visual areas.

The similarity in attentional modulation during the observation of Moving and Stationary Hands is consistent with an earlier behavioral finding by Stürmer and colleagues (2000). In that study, the authors found that observing an action resulted in similar visuomotor priming effects for both moving and stationary hand actions. Together with the present study, these data suggest that observing actions that represent the critical stage of an action – such as its end posture – may activate the action observation network with the same automaticity as observing the entire movement unfolding over time.

In conclusion, the present study systematically investigated the largely neglected issue of how selective attention modulates the processing of observed actions. Our data extend and qualify findings from previous studies, most of which have suggested that observed actions are processed relatively automatically. Previous findings of automaticity based on behavioral data are broadly consistent with the pattern of neural activity within the majority of action observation areas, which may encode observed actions independent of capacity limitations. Crucially, however, at least one node within the action observation network was reliably affected by voluntary attention, as revealed by the sensitivity of the left pars triangularis to attentional load. We suggest that the left IFG (specifically, the pars triangularis) is the locus at which inhibitory activity from higher cortical areas interfaces with the action observation network, and that the susceptibility of the left IFG to attentional modulation reflects our ability to filter task-irrelevant actions during ongoing behavior.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.11.030.

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