The neural substrates of action identification

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Mentalization is the process by which an observer views a target as possessing higher cognitive faculties such as goals, intentions and desires. Mentalization can be assessed using action identification paradigms, in which observers choose mentalistic (goals-focused) or mechanistic (action-focused) descriptions of targets' actions. Neural structures that play key roles in inferring goals and intentions from others' observed or imagined actions include temporo-parietal junction, ventral premotor cortex and extrastriate body area. We hypothesized that these regions play a role in action identification as well. Data collected using functional magnetic resonance imaging (fMRI) confirmed our predictions that activity in ventral premotor cortex and middle temporal gyrus near the extrastriate body area varies both as a function of the valence of the target and the extent to which actions are identified as goal-directed. In addition, the inferior parietal lobule is preferentially engaged when participants identify the actions of mentalized targets. Functional connectivity analyses suggest support from other regions, including the medial prefrontal cortex and amygdala, during mentalization. We found correlations between action identification and Autism Quotient scores, suggesting that understanding the neural correlates of action identification may enhance our understanding of the underpinnings of essential social cognitive processes.

Keywords: fMRI; action identification; mentalize; ventral premotor cortex; extrastriate body area; amygdale

INTRODUCTION

In the movie *Play It Again, Sam*, a gang of motorcyclists accosts Woody Allen, delivers him a sound beating and then runs off with his date. In later describing the incident to his friends, Allen explains: 'I had to teach them a lesson . . . I snapped my chin onto a guy's fist and hit one in the knee with my nose.' Allen's inventive reframing illustrates the wide range of ways that actions—both our own actions and the actions of others—can be described. How observers conceptualize actions varies widely in terms of the level of intentionality and motivation ascribed to the actor. Observers may focus either on behavioral details of an action (the 'means') or on the intentions or consequences associated with it (the 'ends'). Observers who focus more on the intentions or consequences of an action are thought to be mentalizing the actor: accounting for his or her motivations, intentions and complex cognitions (Goldman, 1970; Vallacher and Wegner, 1985; Wegner and Vallacher, 1986). In this study, we assess the neural structures involved in the ascription of motivations and intentions to the actions of others during action identification.

Action identification

Action identification can be assessed using the Behavior Identification Form (Vallacher and Wegner, 1989). This measure allows a respondent who considers another's action (e.g. *Ringing a doorbell*) to select either a higher-level, mentalistic description of it (*Seeing if anyone is home*) or a lower-level, mechanistic description (*Moving a finger*) (Vallacher and Wegner, 1985; Kozak *et al.*, 2006). Higher level identifications predict agreement with mentalistic attributions of thoughts, goals and emotions. Action identification can thus usefully assess mentalization, which is a crucial component of high-level social functioning. Mentalizing deficits characterize serious developmental disorders like autism and Asperger's syndrome that impair social functioning (Baron-Cohen, 1997; Dziobek *et al.*, 2008; Blair, 2008).

Typically, healthy adults mentalize liked others more than disliked others (McPherson-Frantz and Janoff-Bulman, 2000; Malle and Pearce, 2001). This discrepancy is reflected in discrepancies in action identification across targets. Liked targets' actions are consistently identified at higher levels than disliked targets' (Kozak *et al.*, 2006). This suggests that mentalization as assessed by action identification tasks varies as a function of the observer's impression of the actor.

Neural correlates of action identification

The neural correlates of action identification have not yet been identified. Regions that play a role in the inference of intention from actions and those involved in mentalization may be involved, particularly the ventral premotor area,

extrastriate body area, temporo-parietal junction and medial prefrontal cortex. Several recent reviews have assessed the distinct roles these regions play in social cognition (Frith and Frith, 2003; Gallagher and Frith, 2003; Rizzolatti and Fabbri-Destro, 2008; Van Overwalle, 2008).

Both the ventral premotor cortex and the extrastriate body area play roles in the assessment of actions that are seen, heard or imagined (Schubotz and von Cramon, 2004; Hamilton et al., 2006; Urgesi et al., 2007; de Lange et al., 2008). Both regions are particularly active when processing others' goal-relevant behavior (Iacoboni et al., 2005; Takahashi et al., 2008). Relative to the ventral premotor cortex, activity in extrastriate body area is more sensitive to the identity of the actor performing a visually perceived or imagined action (Downing et al., 2001; Astafiev et al., 2004; Schubotz and von Cramon, 2004; Pourtois et al., 2007; Urgesi et al., 2007). For example, the region is progressively less sensitive to actions performed by less human-like actors (e.g. monkey versus dog versus fish). The ventral premotor cortex is active both during the performance and the viewing of an action and so is thought to play a crucial role in mimicry and empathic accuracy via mental simulation of others' actions (Rizzolatti and Craighero, 2004; Iacoboni, 2009). A major function of this region seems to be to derive goals from observed and imagined actions (Iacoboni et al., 2005; de Lange et al., 2008). Finally, a recent meta-analysis (Van Overwalle, 2008) has indicated that the temporo-parietal junction is involved in the attribution of transient mental states such as immediate goals and intentions, as compared to the medial prefrontal cortex, which is primarily engaged in inferring others' enduring dispositions, personality traits or scripts. Of course, because social cognition requires co-activation among these regions, the role of the various structures in distinct mentalization processes may in some cases be difficult to completely distinguish. For example, many false belief tasks elicit activation in both the temporo-parietal junction and the medial prefrontal cortex (Van Overwalle, 2008).

The present study

We conducted an event-related functional magnetic resonance imaging (fMRI) assessment of the neural correlates of action identification. During scanning, participants made high or low identifications of the actions of targets that were described as being likable, neutral or unlikable. We hypothesized that ventral premotor cortex and extrastriate body area would be preferentially involved when participants were making goal-focused, high-level action identifications, but that, in keeping with prior research, the degree of modulation in each area would be affected by contextual cues such as the identity and affective valence of the actor. We also hypothesized that temporo-parietal junction, which is involved in assessing actors' immediate and temporary goals and intentions, would be more active when participants considered likable targets' actions. This prediction follows indications that participants considering others' actions consistently consider the goals and mental states of likable targets more than unlikable targets. Following testing, participants completed the Autism Quotient (Baron-Cohen et al., 2001), and we predicted that participants' action identification scores would predict the extent to which they reported autistic traits.

METHODS

Participants

Twenty-four healthy adult volunteers (12 female, M age = 26.4 years, s.d. = 5.9 years) underwent fMRI scanning. Screening was conducted using the Structured Clinical Interview for DSM Disorders (SCID) to confirm that all participants were free of a current or recent depressive episode or lifetime diagnosis of any other Axis I disorder as well as autism or pervasive developmental disorders, mental retardation or significant medical or neurological disease. All participants were right-handed and medication-free. The study was approved by the National Institute of Mental Health's institutional review board, and all participants provided written informed consent.

fMRI task

The action identification task was an expanded version of the Behavior Identification Form used in previous investigations (Vallacher and Wegner, 1989; Kozak et al., 2006). One hundred and eighty action/high-identification/low-identification triads were generated. An example of one such triad was the action taking a drink listed with the low-level identification swallowing liquid and the high-level identification quenching his thirst. Respondents were asked to indicate for each triad whether the action was better described by the higher or lower level identification. The length of high-level (M = 3.29, s.d. = 1.40) and low-level (M = 3.41, SD = 1.13) phrases were not significantly different (P > 0.10).

During the scan session, three event-related fMRI runs were acquired from each participant. Before each scan session, participants read one of three brief descriptions of a male college student and then were instructed to imagine the particular person that had been described performing each of the actions that would be presented and to decide which of two descriptions would best apply to what that person was doing. One description was of a highly unlikable target, one of a neutral target and one of a highly likable target. For a sample description of a likable target, please see Appendix A. The descriptions were drawn from those used by Kozak et al. (2006) and were matched for length and content. So, for example, whereas the likable target is described as 'friendly' and 'easygoing', these adjectives were replaced with 'quiet' and 'earnest' for the neutral target and 'arrogant' and 'unapproachable' for the unlikable target. The order in which the three runs of the task were completed was counterbalanced across participants.
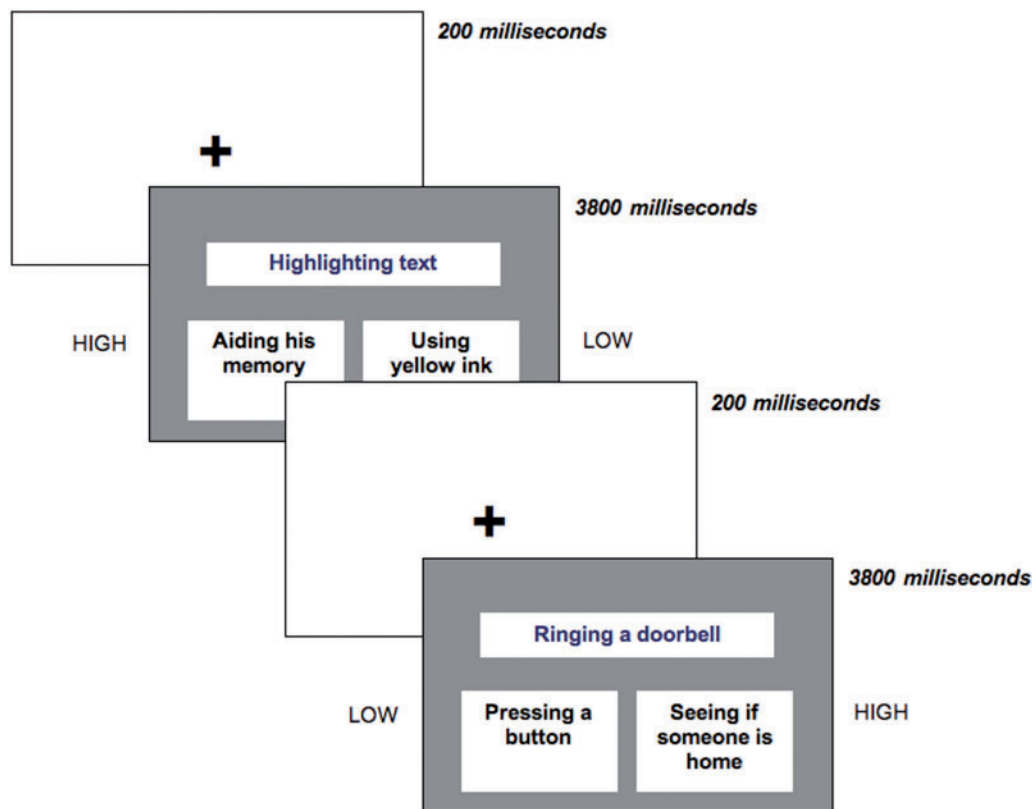
Fig. 1 Sample stimuli as presented to fMRI participants (jittered slides omitted).

Within each run, 60 response choice slides were presented for 3,800 ms each. Each response choice slide displayed the action and two possible response choices (Figure 1). Low-level and high-level identifications appeared on the right and left sides of the screen randomly across trials. Participants identified each action using their right or left thumb. Each response choice slide was followed by a 200-ms fixation cross. Eighty fixation trials (jitters) appeared for 2,000 ms at random intervals. Each run began and concluded with five 2,500-ms baseline fixation trials. Each run used a separate stimulus set and was programmed in E-Studio.

Stimulus images were projected onto a screen that participants viewed in a mirror in the MRI scanner. Participants were placed in a light head restraint within the scanner. (Subsequent analyses indicated that no participant moved more than 4 mm during the scan.)

T2*-weighted images were collected during fMRI scanning using a 1.5-T GE Signa scanner (GE Medical Systems, Milwaukee, WI, USA) (matrix 64×64; repetition time, 2,500 ms; echo time, 20 ms; field of view, 240 mm; voxels, $3.75 \times 3.75 \times 4$). Functional images were acquired with a gradient echo-planar imaging (EPI) sequence (axial plane, 31 contiguous axial slices). High-resolution T1-weighted anatomical images were also acquired (three-dimension Spoiled GRASS with inversion recovery prep pulse; number of 1.5-mm axial slices, 128; field of view, 240 mm; number of acquisitions, 1; repetition time, 8.1 ms, echo time, 1.8 ms; matrix, 256×256).

fMRI pre-processing

Participants with extreme action identification patterns were included in behavioral but not fMRI analyses. These participants' data showed patterns in which, for example, nearly all of the likable targets' actions were identified at high levels, or nearly all of the unlikable targets' actions were identified at low levels. These patterns closely conformed to predicted and previously demonstrated patterns of action identification (Kozak et al., 2006). However, extreme response patterns prevented eight participants from acquiring at least 10 responses in each response category, and their neuroimaging data were excluded to preserve statistical reliability. One additional participant was excluded due to scanner error. The remaining 15 participants included 7 males and 8 females with an average age of 25.0 years (range, 21.4–36.0 years, s.d. = 3.7 years).

Data were analyzed within the framework of the general linear model using Analysis of Functional Neuroimages (AFNI) (Cox, 1996). Both individual and group-level analyses were conducted. The first four volumes in each of the three scan series, collected before equilibrium magnetization was reached, were discarded, leaving 166 TRs per run and 498 TRs total per participant. Data were then motion corrected, normalized and spatially smoothed using an isotropic

6-mm Gaussian kernel. As a result, all signal amplitude and regression coefficients represent a percent signal change from the mean. Regressors for high- and low-action identifications across the three targets were created by convolving the train of stimulus events with a gamma-variate hemodynamic response function to account for the slow hemodynamic response (Cohen, 1997). Linear regression modeling was performed using the full set of regressors to model baseline drift.

Statistical analyses

Voxel-wise group analysis involved transforming single-subject β-coefficients into the standard coordinate space (Talairach and Tournoux, 1988). Following normalization, voxels measured 3 mm³. We conducted a 3 (target) $\times$ 2 (level of action identification) ANOVA to address our specific hypotheses. This random-effects ANOVA was performed on the means of all regressors compared to baseline (fixation) and resulted in group maps of areas of differential activation at a statistical threshold of $P < 0.005$. These clusters were used to define functional regions of interests (ROIs), the labeling of which was determined by Talairach–Tournoux Daemon (Talairach and Tournoux, 1988). Average signal changes in relevant ROIs were extracted and compared using planned contrast tests. This analysis allows for the assessment of the nature of the interaction. Without such follow-up analyses, we know that, for example, target and action identification had an interactive effect within the identified regions but not the nature of this effect. To correct for multiple comparisons in AFNI, a spatial clustering operation was performed using AlphaSim with 1000 Monte Carlo simulations taking into account the entire EPI matrix, with a map-wise false-positive probability of $P < 0.05$.

We conducted two functional connectivity analyses by examining covariation across the whole brain with the activation in two separate seed voxels within functionally defined ROIs identified by the ANOVA. In each cluster, the voxel with peak signal change became a seed voxel, and the time series within this voxel was extracted for each participant. Baseline plus linear and quadratic trends were removed from each voxel's time series. Then a voxel-wise correlation analysis was conducted between each individual voxel's time series and that of the identified seed and the resulting correlation coefficient squared to produce the proportion of signal variation due to correlation with the seed. Correlation coefficients were normalized using a Fisher transformation, and t-tests were performed on these transformed values.

RESULTS

Behavioral results

Manipulation checks were conducted after scanning to confirm that the extent to which participants liked, understood and felt similar to the likable, neutral and unlikable targets
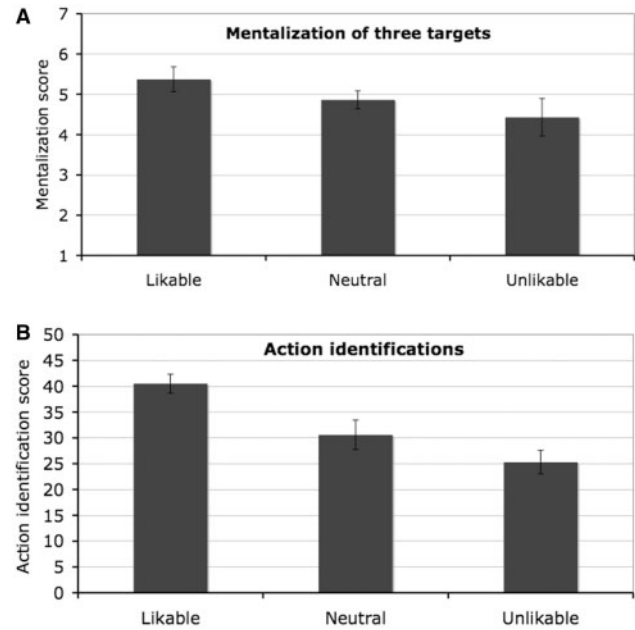

Fig. 2 Behavioral responses to targets as a function of liking. (**A**) Mentalization scores for likable, neutral and unlikable targets. (**B**) Action identification scores for likable, neutral and unlikable targets.

varied as we predicted. Participants were asked these questions about all three targets (e.g. 'How much did you like [likable character's name]?') and answered using seven-point scales. The answers to these questions tend to be highly correlated and are thought to index the extent to which a target is mentalized (Kozak et al., 2006). Calculations of reliability indicated high reliability of these ratings for likable, neutral and unlikable targets (Cronbach's $\alpha = 0.76$, 0.80 and 0.85, respectively), and so ratings were averaged for each target to create mentalization scores. A three-level ANOVA conducted on mentalization scores showed, consistent with Kozak et al. (2006), that participants mentalized likable targets more ($M = 5.38$, s.d. $= 1.03$) than neutral targets ($M = 4.86$, s.d. $= 0.83$), who they mentalized more than unlikable targets ($M = 4.43$, s.d. $= 0.73$), $F(2, 46) = 25.22$, $P < 0.001$ (Figure 2A). (All P-values are reported as two-tailed tests.) Significant differences between likable and neutral targets, $t(23) = 5.46$, $P < 0.001$ and between neutral and unlikable targets, $t(23) = 3.95$, $P < 0.001$, were found. Mentalization patterns and statistical effects for the sub-sample of fMRI participants were highly similar to those for the full group. Here again, participants mentalized likable targets more ($M = 5.60$, s.d. $= 0.91$) than neutral targets ($M = 5.044$, s.d. $= 0.77$), who they mentalized more than unlikable targets ($M = 4.51$, s.d. $= 0.70$), $F(2, 28) = 43.18$, $P < 0.001$. Significant differences between likable and neutral targets, $t(14) = 5.80$, $P < 0.001$ and between neutral and unlikable targets, $t(14) = 6.28$, $P < 0.001$, were observed.

A three-level ANOVA was conducted on the action identification scores (high-level identifications were coded '1' and low-level identifications '0') collected during the fMRI scanning procedure. Analyses showed significant variation in
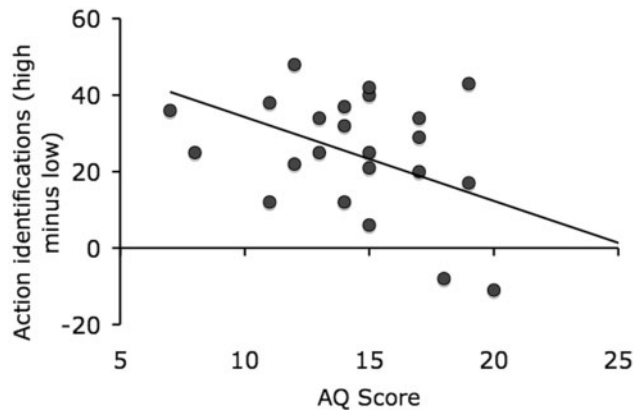
Fig. 3 Correlation between Autism Quotient (AQ) scores and Action Identification scores for likable targets.

action identification patterns across targets, $F(2, 46) = 15.35$, $P < 0.001$. Participants' mean action identification score was 40.5 (s.d. = 8.9) for likable targets, 30.6 (s.d. = 14.0) for neutral targets and 25.3 (s.d. = 11.2) for unlikable targets (Figure 2B). Action identification scores for likable targets were significantly higher than for unlikable, $t(23) = 6.81$, $P < 0.001$ or neutral targets, $t(23) = 3.50$, $P < 0.005$. Scores for neutral targets trended higher than scores for unlikable targets, $t(23) = 2.00$, $P < 0.06$. Patterns and statistical effects of action identification for the sub-sample of fMRI participants were once again highly similar to those for the full group. Participants' mean action identification score was 39.7 (s.d. = 7.0) for likable targets, 32.3 (s.d. = 10.5) for neutral targets and 27.0 (s.d. = 10.6) for unlikable targets $F(2, 28) = 7.85$, $P < 0.005$. Action identification scores for likable targets were significantly higher than for unlikable, $t(14) = 4.01$, $P < 0.001$ or neutral targets, $t(14) = 2.43$, $P < 0.05$. Scores for neutral targets trended higher than scores for unlikable targets, $t(14) = 1.55$, $P = 0.14$.

The mean Autism Quotient score for all participants was 14.86 (s.d. = 4.03). Autism Quotient scores were inversely correlated with the proportion of high-level identifications participants made for likable targets, $r(22) = -0.50$, $P < 0.05$, but not neutral, $r(22) = 0.02$, ns or unlikable, $r(22) = 0.11$, ns, targets. The magnitude of the correlation between Autism Quotient scores and high-level identifications was significantly greater for likable targets than for unlikable targets, $Z = 2.14$, $P < 0.05$ and marginally greater than for neutral targets, $Z = 1.84$, $P < 0.10$ (Figure 3). The relevant effect sizes were similar for fMRI participants, although the reduced sample size resulted in reduced significance levels, respectively, $r(13) = -0.44$, $P < 0.10$; $r(13) = 0.07$, ns; $r(13) = -0.05$, ns. Thus, participants with fewer autistic personality traits were more likely to consider the goals and intentions underlying likable, mentalized targets' actions.

fMRI results

Target × action identification interactions. In AFNI, we conducted a 2 × 3 ANOVA to test neural activation patterns during action identification (high-level vs low-level) for likable, neutral and unlikable targets. An interaction between target and action identification level was identified in the middle temporal gyrus near the extrastriate body area (x, y, $z = 69$, -47, -7), $F(2, 28) = 6.43$, $P < 0.005$ (Figure 4A). Planned contrast tests on average changes in activation were conducted using SPSS and indicated that the activation was greater in this region when participants identified likable targets' actions at high levels relative to low levels, $t(14) = 4.38$, $P < 0.001$. No significant difference was found across levels of action identification for neutral participants ($P < 0.10$). For unlikable targets, a marginally significant effect emerged indicating that this region of middle temporal gyrus was relatively more active when targets' actions were identified at low levels relative to high levels, $t(14) = 1.77$, $P < 0.10$.

In addition, an interaction between target and action identification level emerged in the amygdala (x, y, $z = 23$, -10, -12), $F(2, 28) = 6.43$, $P < 0.005$ (Figure 4B). The pattern of activation in this region corresponded closely to the pattern of activation seen in the middle temporal gyrus, with planned contrasts conducted in SPSS showing that high-level identifications for likable targets resulted in higher activation than for neutral or unlikable targets, $t(14) = 2.98$, $P < 0.01$. Greater activation was also seen in the amygdala in response to neutral targets' high-level identifications, $t(14) = 2.43$, $P < 0.05$, whereas the reverse pattern was seen for unlikable targets, $t(14) = 2.39$, $P < 0.05$. For a complete list of regions identified by the ANOVA, see Table 1.

In support of the interpretation that amygdala activation corresponded to activity in the extrastriate body area, we conducted a functional connectivity analysis that used a seed voxel in the amygdala identified using the ANOVA interaction effect. We selected this voxel due to the strong body of literature suggesting that the amygdala plays a very early role in the assessment of valence information and that the input that cortical regions like the middle temporal gyrus receive from the amygdala aid in their interpretations of targets' behaviors (Morris, 1998; Iidaka et al., 2001; Cheng et al., 2007; Peelen et al., 2007; Van Overwalle, 2008). The results of this analysis showed heightened functional connectivity ($P < 0.005$) in a region proximate to the region of middle temporal gyrus identified in the interaction effect from the ANOVA (x, y, $z = 47$, -55, -3). For a complete list of regions identified by this connectivity analysis, see Table 2.

An interaction between target and level of action identification was also found in the ventral premotor cortex (x, y, $z = -37$, 16, 26), $F(2, 28) = 6.43$, $P < 0.005$ (Figure 4C). Planned contrast tests conducted in SPSS indicated that activation was greater in this region when participants identified unlikable targets' actions at high relative to low levels, $t(14) = 2.30$, $P < 0.05$. No significant difference was found across levels of action identification for neutral participants ($P < 0.10$). For likable targets, ventral premotor cortex was
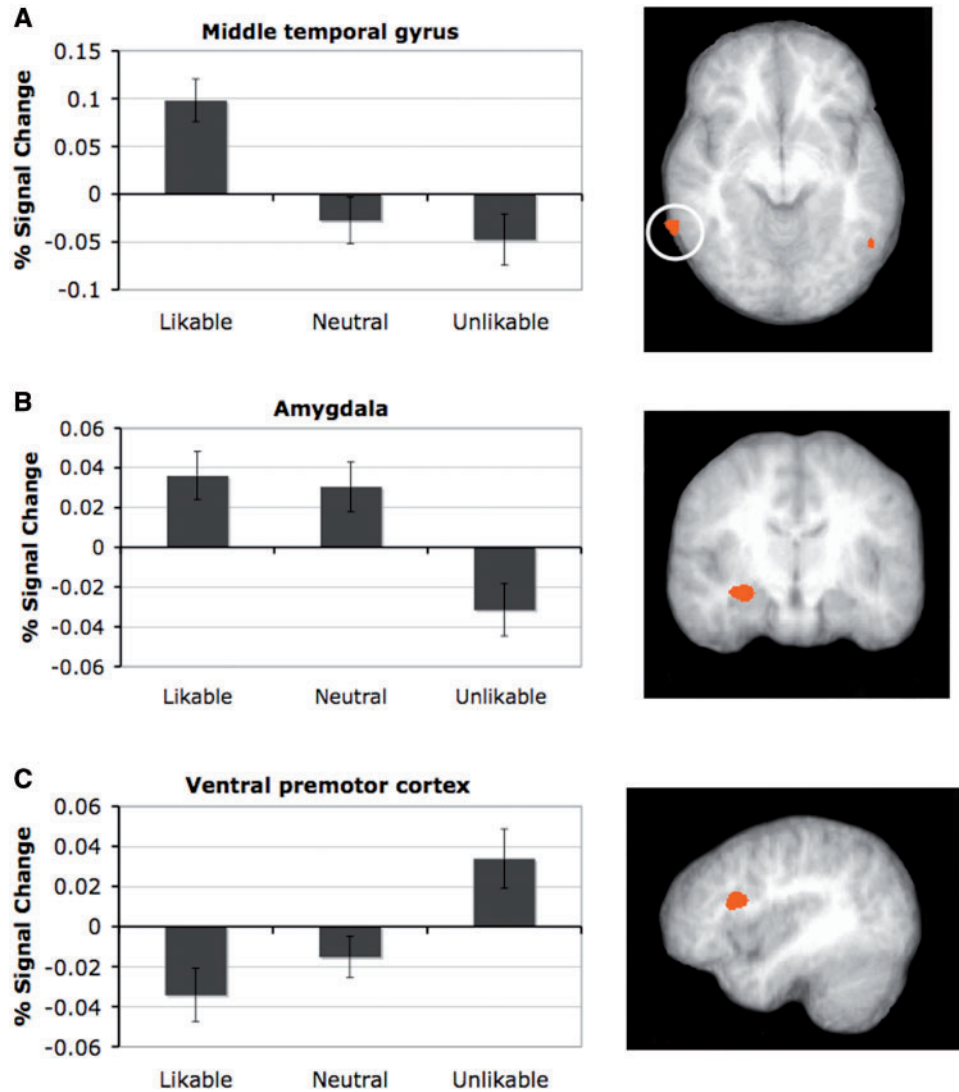
Fig. 4 Regions obtained from random-effects analysis of the target × action identification interaction effect. Scores on the *Y* axis represent percent signal change for actions identified as high-level minus percent signal change for actions identified as low level. (**A**) A region of the middle temporal gyrus near the extrastriate body area showing relatively greater activation when participants identified likable targets' actions at high levels than when they identified unlikable targets' actions at high levels. (**B**) A region of the amygdala showing a similar pattern to that observed in the extrastriate body area. (**C**) A region of ventral premotor cortex showing a pattern opposite to that observed in middle temporal gyrus and amygdala; here, relatively more activation was observed when participants identified unlikable targets' actions at high levels.

relatively more active when targets' actions were identified at low levels relative to high levels, $t(14) = 2.56$, $P < 0.05$.

Main effect of target. A main effect of target, $F(2, 28) = 6.43$, $P < 0.005$, was found in the left inferior parietal lobule (BA 40; *x, y, z* = −56, −53, 55) (Figure 5). Follow-up contrast tests in AFNI confirmed that this was the only brain region that was significantly more active when considering likable as compared to both neutral (*x, y, z* = −56, −53, 55) and unlikable (*x, y, z* = −53, −56, 58) targets' behavior, $t(14) = 3.05$, $P < 0.005$. The observed pattern of activation was corroborated by planned contrast tests conducted in SPSS, which indicated that average activation in this region was higher when participants identified the actions of likable targets relative to either neutral, $t(14) = 4.89$, $P < 0.001$ or dementalized, $t(14) = 3.16$, $P < 0.01$, targets.

The results of a connectivity analysis revealed that the region of inferior parietal lobule identified by the ANOVA showed increased connectivity during the task with regions that are associated with the inference of mental states and intentions, including the medial prefrontal cortex (BA 10) and right temporal pole (Gallagher and Frith, 2003; Gallese *et al.*, 2004; Hamilton *et al.*, 2006; Mitchell *et al.*, 2006; Hooker *et al.*, 2008; Van Overwalle, 2008). For a complete list of regions identified by this functional connectivity analysis, see Table 2.

The main effect results of the ANOVA also revealed several regions in which activation increased when participants were considering the actions of unlikable as compared to neutral or likable targets (Table 1). These regions included the anterior insula and dorsal anterior cingulate cortex. Only

Table 1 Coordinates of peak activations and *F*-values for regions demonstrating a significantly different BOLD response for targets as a function of target and target × action identification

Region	BA	L/R	Voxels	F	x	y	z
Main effect of target							
Likable > Unlikable							
Inferior parietal lobule	40	L	11	9.39	−56	−53	55
Unlikable > Likable							
Inferior frontal gyrus	46	L	13	6.45	−46	29	14
Cingulate gyrus	32	R	16	6.73	14	29	30
	24	L	17	6.48	−7	13	32
Insula	13	L	19	7.86	−34	17	3
	13	R	61	8.34	41	2	−5
	13	R	13	7.08	44	−21	21
Cingulate gyrus	24	L	26	9.17	−7	3	42
Middle frontal gyrus	6	R	177	7.81	32	−4	54
Superior temporal gyrus	22	L	35	7.07	−53	−14	8
	22	R	38	8.48	69	−58	15
Precentral gyrus	6	L	18	6.68	−25	−23	66
Inferior parietal lobule	40	R	34	6.99	47	−30	30
	40	R	15	6.72	47	−44	52
Inferior temporal gyrus	37	R	34	7.50	57	−59	−12
Middle occipital gyrus	19	R	22	6.63	44	−75	−6
Inferior occipital gyrus	18	R	12	6.89	41	−87	−13
Target × action identification							
Ventral premotor cortex (inferior/middle frontal gyrus)	9/45	L	35	8.72	−37	16	26
Amygdala		R	25	7.51	23	−10	−12
Middle temporal gyrus	21/37	R	22	6.64	69	−47	−7

Activations significant at *P* < 0.005, corrected for multiple comparisons at *P* < 0.05.

one region showed preferential action as a main effect of action identification level, $F(1, 14) = 11.07$, $P < 0.005$. This was a region of middle frontal cortex (BA 8; *x, y, z* = −46, 28, 46). Activation in this region was greater when participants made high-level identifications relative to low-level identifications.

DISCUSSION

The present study found, in keeping with prior findings (Kozak *et al.*, 2006), that the actions of likable targets are mentalized more than the actions of disliked targets and that the extent to which this is true is negatively correlated with scores on the Autism Quotient (Baron-Cohen *et al.*, 2001). Individuals with more self-reported autistic traits are less likely to show the typical pattern of attributing intentionality and goal-directedness to likable targets.

The action identification task generated activation in regions previously associated with attention to others' goals and intentions and with the interpretation of others' perceived or imagined actions. High-level action identification of likable actors' behaviors preferentially recruited activation in a region of middle temporal gyrus near the extrastriate body area and in the amygdala. High-level identifications of unlikable actors' behaviors recruited relatively more activation in ventral premotor cortex. The inferior parietal lobule was more active during identifications of

likable actors' behavior than during identification of neutral or unlikable dementalized actors' behavior.

Extrastriate body area

An interaction between the identity of the target and action identification level was found in three regions: middle temporal gyrus near the extrastriate body area, ventral premotor cortex and the amygdala. The extrastriate body area is a region of lateral occipito-temporal cortex that was originally identified as responding selectively to visual images of human bodies and body parts (Downing *et al.*, 2001; Schubotz and von Cramon, 2004). Research suggests that the region also responds to body movements that are imagined or executed by one's own body (Astafiev *et al.*, 2004). This suggests that, rather than being a region that processes low-level visual information, the extrastriate body area integrates multisensory information about bodies and actions (Astafiev *et al.*, 2004; Jeannerod, 2004; Arzy *et al.*, 2006; Peelen *et al.*, 2007; Urgesi *et al.*, 2007).

Responsiveness in the extrastriate body area is heavily dependent on the identity of the actor. The region is more sensitive to movements and representations of humans than to successively less human-like actors (Downing *et al.*, 2007; Pourtois *et al.*, 2007). This suggests that extrastriate body area is relatively more involved in interpreting actions for which the actor's identity is more salient (Urgesi *et al.*, 2007;

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Table 2 Regions in which activation varies as a function of signal change in amygdala and temporo-parietal junction

Region	BA	L/R	Dir	t	x	y	z
Amygdala seed							
Medial frontal gyrus	10	L/R	−	4.39	19	71	8
Middle frontal gyrus	10	L	−	3.83	−37	53	−4
Inferior parietal lobule	2/40	L	+	3.40	−43	−29	27
Supramarginal gyrus	40	L	−	3.56	−62	−52	36
Middle temporal gyrus	37/19	R	+	3.56	47	−55	−3
	19	R	+	3.38	37	−63	10
	39	L	+	3.45	−39	−68	23
Precuneus	19	L	−	3.92	−7	−88	39
Cuneus	18	L/R	−	3.40	1	−99	14
Temporo-parietal junction seed							
Medial frontal gyrus	11	R/L	+	3.40	11	62	−16
	6	R	−	3.36	7	3	55
Middle frontal gyrus	10	R	+	3.33	41	62	10
	10	R	+	3.40	21	58	25
	46	R	+	4.34	54	46	11
	11	R	+	3.42	35	35	−15
Superior frontal gyrus	10	R	+	3.40	21	58	25
	10	R	+	3.61	35	52	20
Superior frontal gyrus	6	R	−	3.43	5	6	68
Inferior frontal gyrus	47	R	+	3.34	54	36	0
	45	R	+	3.46	54	26	6
Middle temporal gyrus	21	R	+	4.42	60	4	−12
Fusiform gyrus	20	R	−	3.37	49	−10	−29
	20	L	−	3.87	−45	−35	−21
	19	R	−	4.57	23	−56	−15
	19	L	−	3.50	−27	−62	−13
Middle temporal gyrus	22	R	−	6.63	45	−25	−9
	37/21	R	−	3.92	60	−52	−8
Inferior parietal lobule	40	R	−	3.33	66	−43	24
Posterior cingulate gyrus	30	R/L	−	3.57	−3	−55	4
Inferior occipital gyrus	19	R	−	4.49	37	−77	−12
Precuneus	19	R	−	3.81	33	−79	33
Middle occipital gyrus	19	R	−	5.04	33	−82	7
Cuneus	18	L	−	4.15	−5	−88	6
	19	L	+	4.05	−17	−95	28
	18	L	+	3.92	−27	−96	−8
Inferior occipital gyrus	18	L	+	3.98	−41	−89	−8

Activations significant at $P < 0.005$, corrected for multiple comparisons at $P < 0.05$.
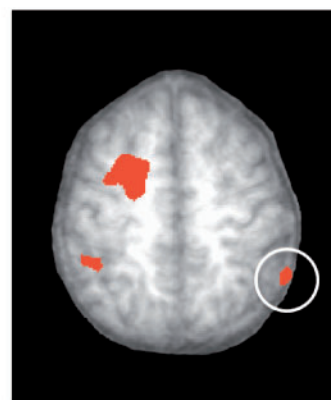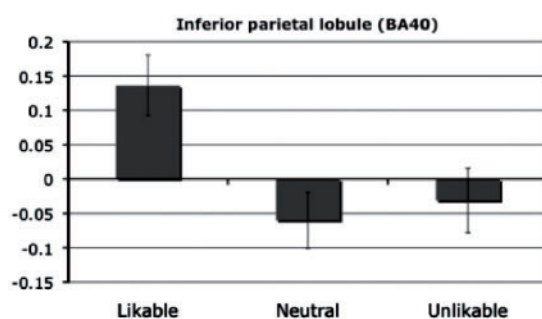

Fig. 5 A region of inferior parietal lobule obtained from random-effects analysis of the main effect of target. Scores on the *Y* axis represent percent signal change for likable, neutral and unlikable actors.

Myers and Sowden, 2008) but see (Morris *et al.*, 2006). The extrastriate body area may be geared to take into account the social meaning of actions, so that actions can be understood *with reference* to the person executing them (Jeannerod, 2004; Blake and Shiffrar, 2007). Higher-level action identifications (e.g. identifying *Highlighting text* as *Aiding his memory*) by definition require mentalization and individuation of the actor, whereas mechanistic action identifications (e.g. *Using yellow ink*) require no reference to identity for their interpretation. This may be why participants showed relatively heightened activation in the extrastriate body area when making high-level identifications of likable targets' actions.

Downing and colleagues (2001) originally identified the central coordinates of the extrastriate body area as *x, y, z* = 51, −71, 1. The region of middle temporal gyrus identified in the present study did not overlap with this voxel. However, our coordinates were proximal to those identified in several other studies investigating responses to moving bodies and identified as extrastriate body area, including Arzy *et al.* (2006), *x, y, z* = 54, −55, 1; and Astafiev *et al.* (2004), *x, y, z* = 45, −57, 11. We interpret the identified region of activation as performing a function comparable to that described in assessments of the extrastriate body area. The fact that our task featured verbal descriptions of actions rather than visually depicted actions may help to account for the disparity in anatomical location.

Corroborating this interpretation of activation patterns in the middle temporal gyrus is the similar pattern of activation seen in the amygdala during the identification of the various targets' actions. The amygdala plays a key role in making trait inferences about others that are related to affective valence, such as trustworthiness (Said *et al.*, 2008). And results of prior studies have suggested that emotionally evocative body movements increase activation in the extrastriate body area, which appears to result from its functional connections with the amygdala (Cheng *et al.*, 2007; Peelen *et al.*, 2007). This suggests that the extrastriate body area receives emotional inputs from the amygdala during action identification and that this input aids in the formation of evaluations about the targets' behaviors (Van Overwalle, 2008). The involvement of the amygdala in action identification conforms to longstanding theories about the amygdala's role in social cognition (Adolphs, 1999; Bar-On *et al.*, 2003; Corden *et al.*, 2006). Based on our data, we concur with suggestions by Amaral and colleagues (2003) that affective processing in the amygdala may play a supporting role during mentalization but may not be central to the process.

Ventral premotor cortex

In contrast to the activation patterns seen in the middle temporal gyrus and amygdala, the ventral premotor cortex responded preferentially during high-level identifications of *unlikable* targets' actions. This nearly reciprocal pattern of activation in the middle temporal gyrus and the ventral

premotor cortex is extremely similar to reciprocal patterns of activation seen in these regions in numerous studies in which participants make inferences about others' actions (Hamilton *et al.*, 2006; Urgesi *et al.*, 2007; de Lange *et al.*, 2008). This suggests that these regions play complementary roles in action identification. Unlike the extrastriate body area, the ventral premotor cortex may play a greater role in interpreting actions when the actor is relatively more depersonalized.

The ventral premotor area is a component of the mirror neuron network (Iacoboni *et al.*, 2005; Lotze *et al.*, 2006). Recent research has led investigators to conclude that this region of the mirror system is primarily responsive to an action's goals rather than to the specific actions required to achieve the goal (Gazzola *et al.*, 2007; Rizzolatti and Fabbri-Destro, 2008). Studies involving action observation may be more likely to result in mirror-system activation when intentionality must be inferred from the actions (Iacoboni *et al.*, 2005; Hamilton *et al.*, 2006). Ventral premotor cortex may be involved in mentally simulating goal-directed actions, which does not appear to require high-level symbolic representations of an action, but only rudimentary coding of its anticipated end-state (Gallese *et al.*, 2004; Van Overwalle, 2008). This conforms to the present finding that the ventral premotor cortex is relatively more responsive during high-level action identifications of unlikable actors, as high-level identifications are those that consider an action's underlying goals and intentions. The region identified in the present study (*x, y, z* = −37, 16, 26) is highly proximal to the region identified in recent studies that assess responses on actions and intentions, for example, de Lange et al., 2008 (*x, y, z* = −36, 20, 22); Buccino *et al.*, 2004 (*x, y, z* = 40, 12, 24); and Urgesi *et al.*, 2007 (*x, y, z* = −58, 11, 24).

The motor mapping process in which ventral premotor cortex is engaged is relatively unrelated to the identity of the acting body (Jeannerod, 2004; Urgesi *et al.*, 2007). Jeannerod (2004) has proposed that the ventral premotor cortex is primarily engaged in responding to actions and their implied goals rather than to the individual performing the action. This is in contrast to the extrastriate body area, which, he proposes, is where the mental processes implied by others' actions may be decoded so that the accompanying intentions or emotions of others can be understood. The extent to which likable actors are more mentalized and personalized may explain why a region of middle temporal gyrus near the extrastriate body area is relatively more involved in identifying their actions at high levels, while ventral premotor cortex plays a relatively larger role in identifying unlikable actors' behaviors.

Inferior parietal lobule

The present behavioral data confirm prior findings that the actions of unlikable actors are interpreted as less driven by goals and intentions and as more mechanical and mindless

than the actions of likable actors (Kozak *et al.*, 2006). The sole cluster in which activation was observed to increase when participants interpreted the behaviors of likable as compared to unlikable actors was a cluster in the inferior parietal lobule. We predicted that the main effect of target would reveal activation changes in the temporo-parietal junction, a region that extends from the superior temporal sulcus to the inferior parietal lobule and is active during the inference of intentions on the basis of others' movements or behaviors (Saxe and Wexler, 2005; Van Overwalle, 2008). A recent meta-analysis indicated that the temporo-parietal junction is most reliably activated when study participants engage in tasks involving the detection of agency and the inference of goals or end states for described actions (and that both left and right temporo-parietal junction are active in tasks requiring goal inferences) (Van Overwalle, 2008). This is also consistent with prior findings that the temporo-parietal junction is more engaged in interpreting the actions of human than animated agents (Mar *et al.*, 2007). Data from the meta-analysis conducted by Van Overwalle (2008) indicate that tasks that assess agency or action goals identify inferior parietal lobule clusters that are dorsal (mean $z = 42$ and 28, respectively) to those identified by standard theory of mind tasks (mean $z = 22$).

However, the central coordinates typically defined as the temporo-parietal junction in previous studies are 1–3 cm ventral to those identified in the current study, and so our results cannot be clearly interpreted as reflecting increased activation of the temporo-parietal junction during the interpretation of likable targets' actions. Alternate interpretations might reflect the findings of Mitchell (2008), which is that the inferior parietal lobule is modulated by general attention demands. Changes in activation as a function of attentional demands have also been observed near the region we identified in this study (LaBar *et al.*, 1999) Plausibly, attention to aspects of the task varied across conditions in the present study.

Other regions involved in mentalization

The medial prefrontal cortex is thought to play a key role in mentalization, perhaps integrating socially relevant information such as trait inferences and scripts (Leslie *et al.*, 2004; Amodio and Frith, 2006; Van Overwalle, 2008). The present study did not show a main effect of actor or level of action identification in this region, although the task required that participants draw on information about the actors' personality traits. This may have been reflected in the results of our connectivity analysis, which revealed enhanced connectivity between the inferior parietal lobule and the medial prefrontal cortex during the task. Coordinated activity in the inferior parietal lobule and medial prefrontal cortex may facilitate inferences about targets' likely goals and intentions based on stored trait representations.

Activation in several regions increased when participants considered the actions of disliked targets. These regions

included the bilateral dorsal anterior cingulate cortex, bilateral anterior insula and right ventrolateral prefrontal cortex. These are regions consistently associated with negative emotions such as disgust, anger and pain (Blair *et al.*, 1999; Murphy *et al.*, 2003; Botvinick *et al.*, 2005; Jackson *et al.*, 2005). Increased activation in these regions suggests considering the actions of the unlikable targets is associated with the generation of negative affect.

Limitations

Several limitations should be considered when assessing the results of the present research. For one, the central coordinates of the inferior parietal lobule cluster identified by the main effect of the ANOVA indicate that this cluster extends outward beyond the masked region of the cortex in addition to extending into BA 40. Our confidence in the validity of the pattern of activation observed in this cluster is enhanced by several factors, including the fact that increased activation in this region in response to mentalized targets' actions would be clearly predicted on the basis of prior findings; the strong effect size observed in this cluster ($F = 9.66$); and the results of the connectivity analysis suggest that this region is functionally connected to other regions consistently implicated in mentalizing, including the medial prefrontal cortex and temporal pole. However, a replication of the present paradigm would help to confirm the precise location and boundaries of the cluster and establish its reliability.

In addition, future research might address the process of action identification more generally. The present task incorporated actors of different valences due to strong suggestions that the cognitive processes involved in interpreting these actors' behaviors varies. Prior behavioral research on action identification indicates that behaviors are interpreted as relatively more goal-directed or mechanical as a function of the target's valence (and status as either mentalized or dementalized) (Kozak *et al.*, 2006). And prior neuroimaging research on the interpretation of actions indicates that extrastriate body area and ventral premotor cortex are differentially involved in interpreting actions as function of whether the target is personalized or depersonalized (Jeannerod, 2004; Downing *et al.*, 2007; Pourtois *et al.*, 2007). However, assessing the process of action identification independent of the target's valence (using, e.g. only neutral targets) would aid in interpreting the current results. It is plausible that if, for example, such a proposed study found ventral premotor cortex to be preferentially activated during low-level identifications of a neutral target that the observed patterns in this study could be re-interpreted as reflecting low-level aspects of likable actors.

An additional worthwhile direction for future research would be a study in which participants did not identify the levels of the actions they saw in one condition so that this condition could be compared with the two conditions assessed in this study. This might assist in expanding the understanding of the neural structures involved in action

identification regardless of the level at which the action is identified.

CONCLUSIONS

We propose, based on the results of the present study, that action identification is carried out by regions that are involved in the interpretation of actions and the inference of their attendant goals, primarily the middle temporal gyrus near the extrastriate body area, the ventral premotor cortex and the inferior parietal lobule. The middle temporal gyrus may be preferentially involved in interpreting the goals of actions when the actor's particular identity is more salient and thus more relevant to decoding the action's meaning, whereas the ventral premotor cortex, which is less sensitive to the identity of the actor, may be relatively more involved in decoding actions for actors who are dementalized, rending the interpretation of the action less reliant on the actor's particular mental characteristics. These regions have frequently been observed to act in conjunction, wherein increasing activation in one is associated with decreasing activation in the other, across a variety of tasks in which participants observe or imagine actions that vary in their goal-directedness (Hamilton *et al.*, 2006; Urgesi *et al.*, 2007; de Lange *et al.*, 2008). The action identification paradigm we report demonstrates that these regions are also active when participants read descriptions of actions rather than view pictures of them, and when they identify how goal-directed versus mechanical they are. The amygdala, inferior parietal lobule and medial prefrontal cortex may play supplementary roles in this process.

Correlations between action identification scores and scores on the Autism Quotient suggest that identifying the neural correlates of action identification may reveal important aspects of human social cognition. Higher Autism Quotient scores were associated with a failure to ascribe high-level identifications to the actions of likable targets—in other words, a failure to infer that intentions and goals underlie their actions. The present research links the performance of a task that requires intact functioning in several regions of the 'social brain' to the presence of autistic spectrum traits. Future research may be able to more precisely identify the neural mechanisms that link mentalization and action identification to the ability to function effectively in the social world.

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APPENDIX A

Sample instructions for a run in which subjects identified the actions of a likeable character.

Please read the following description of a person named ROBERT:

Robert is a 20-year-old student at a large state university. He majors in biology, and he is also interested in political science. Outside class, he participates in intramural sports, because he enjoys getting exercise and being part of a team. On weekends, Robert likes to go to parties and spend time with friends or with his family. Most people find Robert to be friendly and easygoing. Recently, Robert received an award from his school. He tutored several classmates in biology class and helped them to improve their grades. The professor learned that Robert was helping his classmates without asking for any pay in return and told the university. Robert received a service award from the university. This is not the first time that Robert has been recognized for helping others. In high school, Robert's volunteer works helping children with their reading earned him a small scholarship prize.

In this run, please imagine that Robert is the person performing the behaviors. If Robert were performing the following actions, which of the two descriptions would best apply to what he was doing?