Watching people interact:

The neural bases of understanding social relations

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Running title: fMRI of social relations

Summary

The study of human social relationships suggests that they can be classified into four basic forms. We used fMRI to study brain activity while subjects watched two types of social relationships, Communal Sharing (CS) and Authority Ranking (AR). Our aim was to describe the neural mechanisms that allow people to understand everyday social interaction. Subjects were asked to simply watch professionally prepared movie clips depicting everyday interactions. There were 18 clips depicting CS relationships in which the actors were socially equivalent in some respect and 18 clips depicting AR relationships in which there was a hierarchical differentiation between the actors. Each clip was composed of 12 seconds of 'baseline' during which one person appears, followed by 8 seconds of a 'relational' segment during which this person interacts with another person. In between clips, subjects saw a blank screen for 20 seconds (rest). Emotional content and amount of speech were roughly balanced between AR and CS clips and between baseline and relational segments; a behavioral study preceding the imaging study confirmed this balance.

Compared to rest, both AR and CS 'baseline' segments activated a large bilateral network of brain regions encompassing occipital, temporal, premotor (including pars opercularis and triangularis), medial prefrontal (BA 9/10), orbitofrontal and amygdalar regions. Notably, dorsolateral prefrontal and anterior cingulate cortices were not activated. A substantially identical network was also activated while subjects watched both CS and AR 'relational' segments, compared to rest. The only substantial difference was the additional activation of the precuneus while watching two people interacting in both CS and AR relationships. A comparison of 'relational' segment vs. 'baseline' revealed a similar bilateral network for both CS and AR, with generally stronger brain responses to AR. This network was composed by extrastriate, superior temporal and anterior temporal, premotor (including pars opercularis and triangularis), medial prefrontal cortex (BA 9/10), and precuneus. Finally, the direct comparison of the AR versus CS 'relational' parts revealed that the AR relationships produced greater bilateral activation in the superior and anterior temporal cortex,

inferior frontal cortex, and mesial frontal areas (BA 9/10). CS relationships did not yield any additional activation, compared to AR relationships.

The networks observed in our study suggest that we interpret social relationships by understanding actions of others (superior temporal cortex) in agent-independent terms ('mirror' mechanisms in premotor cortex). We encode these actions as embedded in a meaningful context (anterior temporal cortex) and we map these actions onto their relational meaning by drawing on events in our own experience in similar relationships (precuneus).

Key Words: temporal pole – precuneus – superior temporal sulcus - mirror neurons – social cognitive neuroscience – relational models – social interaction

Introduction

The capacity to navigate the social world, to appreciate the intentions behind observed behavior, and to recognize the relationships that exist between people invokes some of the most complex processing that humans perform. Yet phenomenologically these various forms of social cognition occur effortlessly most of the time. These abilities have intrigued philosophers and scientists throughout the ages; however, in the era of modern science only social scientists have studied these abilities in humans. In the past decade, there has been a sea change in the way these abilities are studied as social science theory meets neuroscience methods in the novel field of social cognitive neuroscience.[1, 5, 23, 32] Using neuroimaging, along with neuropsychology and computational modeling, social scientists now have unparalleled access to the operations of the intact hardware of the human mind.

Single-unit studies performed on primates have inspired some of the work on the neural bases of human social cognition. Several of these studies have recently isolated neural mechanisms in the primate brain that allow for the detection and analysis of socially relevant stimuli. Perrett's group has described over the years neurons in the superior temporal sulcus of the macaque brain that respond to hand-object interactions, gaze direction and head orientation, and faces.[34-36] Rizzolatti's group has described a fronto-parietal network for action recognition composed of neurons that fire when the monkey performs an action and when it observes the same action performed by others (mirror neurons).[6, 12, 39, 40] Imaging studies have suggested that the human superior temporal, inferior frontal, and posterior parietal cortex may have similar neural properties to the macaque, albeit certainly evolved.[17, 18] This recent neurophysiological and neuroimaging evidence, coupled with classical behavioral neurology observations that suggest that lesions in some brain regions are associated with a disruption of some aspects of social behavior, creates a solid framework in which it is possible to study how the primate brain encodes social relationships. Prior neuroscience research has examined the mechanisms responsible for coding individual social

entities or particular socially-relevant behaviors. The present study initiates a research program investigating the neural mechanisms that allow for the understanding of social relationships *between* individuals. Perception of a person is very likely to evoke cognition about that person's actual or potential relationships with the perceiver or others. But relationships are not properties of individuals—relationships emerge in the context of coordinated systems of interaction. Each person participates in many distinct relationships with different partners, or with the same partners in different contexts.

When people interact in a social context, they seem to do so according to some basic forms of social relationships. Relational models theory posits that people use four elementary models to construct, interpret, coordinate, plan, recall, and evaluate most social relationships.[8, 9, 16] Over 30 studies have demonstrated the central role of the four relational models in structuring everyday cognition about real relationships, as well as the heuristic value of the theory for interpreting a great variety of social phenomena in diverse cultures. For example, studies show that these four relational models shape patterns of substitutions in naturally occurring social errors in five cultures, as well as intentional social substitutions and order of recall of acquaintances in American subjects. The four models are Communal Sharing, Authority Ranking, Equality Matching, and Market Pricing. When people organize some aspect of a relationship by Communal Sharing, they focus on what they have in common, the ways that they are equivalent to each other, or the importance of the group, (regardless of the real individual differences that participants perceive as well). When people structure a relationship in Authority Ranking, they construct a linear hierarchy that differentiates people according to legitimate power, prestige, or privilege. In Equality Matching, people keep track of the differences among them and know what should be done to reach an even balance, for example by taking turns, dividing things equally, making in-kind exchanges, or wreaking vengeance in tit-for-tat retaliation. Market Pricing allows people to orient to socially meaningful ratios such as prices, wages, rents, or interest rates; money may be the medium but many Market Pricing relationships involve a calculus of non-monetary costs and benefits. People combine these four models to construct complex relationships and institutions. Indeed, it is the implementation of these four

models in diverse ways that generates the innumerable social practices we find within and across cultures. Several studies have shown that the relational models organize diverse aspects of everyday cognition about natural interactions. Here, we used fMRI to start investigating how the human brain encodes Communal Sharing and Authority Ranking relationships.

To do so, we used a research approach that combined the control of a laboratory experiment yet maintained ecological validity. We worked with a team of professional writers, directors, actors, camera, sound, lighting crews and editors to create a set of highly realistic movie clips depicting everyday interactions that are typical of naturally occurring Communal Sharing or Authority Ranking relationships in American culture. Subjects were instructed to simply watch these movie clips as their brain activity was imaged. We used this approach to approximate the way people encode and understand the social interactions they observe in everyday life.

Methods

Subjects

13 right-handed subjects (7 females, mean age 27.2 ± 3.98) were recruited through newspaper advertisements. Participants gave informed consent following the guidelines of the UCLA Institutional Review Board. Handedness was determined by a questionnaire adapted from the Edinburgh Handedness Inventory.[33] All were screened to rule out medication use, a history of neurological or psychiatric disorders, head trauma, substance abuse or other serious medical conditions.

Image acquisition

Images were acquired using a GE 3.0T MRI scanner with an upgrade for echo-planar imaging (EPI) (Advanced NMR Systems, Inc.). A 2D spin-echo image (TR = 4000 ms; TE = 40 ms, 256 by 256, 4-mm thick, 1-mm spacing) was acquired in the sagittal plane to allow prescription

of the slices to be obtained in the remaining sequences. This sequence also ensured the absence of structural abnormalities in the brain of the enrolled subjects. For each subject, a high-resolution structural T2-weighted echo-planar imaging volume (spin-echo, TR = 4000 ms, TE 54 ms, 128 by 128, 26 slices, 4-mm thick, 1-mm spacing) was acquired coplanar with the functional scans. Nine functional EPI scans (gradient-echo, TR = 4000 ms, TE = 25 ms, flip angle = 90, 64 by 64, 26 slices, 4-mm thick, 1-mm spacing) were acquired, each for a duration of 3 minutes and 16 seconds. Each functional scan covered the whole brain and was composed of 49 brain volumes. The first four volumes were not processed due to initial signal instability in the functional scan. The remaining 45 volumes corresponded to five rest periods (blank screen) and four task periods (video clips), all of 20 seconds each. In each scan there were two clips of AR relationships and two clips of CS relationships. The order of presentation of AR and CS clips was counterbalanced across scans and subjects.

Data processing

GE image files were converted into Analyze files. Each functional volume was re-aligned to the T2-weighted structural volume within each subject using a rigid-body linear registration algorithm.[47] The T2-weighted structural volume of each subjects was subsequently warped into a Talairach-compatible[42] MR atlas[46] with fifth-order polynomial nonlinear warping.[48] Finally, the combination of the re-alignment of each functional volume onto the structural volume, and of the warping of the structural volume into the MR atlas, allowed reslicing of functional volumes into the Talairach-compatible MR atlas space. Functional volumes resliced into the MR atlas space were smoothed using a Gaussian filter producing a final image resolution of 8.7 mm by 8.7 mm by 8.6 mm.

Stimuli and instructions

Stimuli consisted of a set of 36 video clips of everyday events that were professionally written, produced, acted, directed, digitally filmed, and edited. The video clips were interleaved with 20 seconds of blank screen (rest periods). Each clip was composed of a 'baseline' period of twelve seconds (corresponding to three brain volumes acquired with a TR=4000 msec) during which a single actor is visible, followed by a 'relational' period of eight seconds (corresponding to two brain volumes acquired with a TR=4000 msec) in which the first actor interacts with a second actor. For half of the clips, the relational period reflected a CS relationship between the actors. For instance, in one CS clip, the two actors are watching family photos. For the other clips, the relational period reflects an AR relationship. For instance, in one AR clip, the two actors are in the library and the librarian tells the student to keep it quiet. The set of stimuli was roughly balanced for amount of speech and emotional subjects participating in the behavioral pre-testing were asked to categorize the 36 video clips as AR or CS, content. Behavioral pre-testing prior to the imaging experiment on a separate sample of subjects confirmed this balance. Further, when asked to categorize the 36 video clips as AR or CS, each subject participating in the behavioral pre-testing reached an accuracy level at 95% or higher.

Subjects participating in the imaging study were instructed to simply watch the video clips. No explanation was given to them about AR and CS models. In a post-imaging interview, some of the subjects stated that they were aware that the clips depicted different kinds of relationships, but none were able to clearly articulate the communal and hierarchical typology.

Statistical analyses

All statistical analyses were performed on the group data after spatial normalization and smoothing. Contrast analyses were based on an analysis of variance (ANOVA) model,[49] which factors out the between-subject and the scan-to-scan variability in signal intensity.[17-21] The dependent variable of the ANOVAs was the signal intensity at each voxel. The alpha level was set at each voxel at p=0.001, uncorrected for multiple spatial comparison. To prevent type I errors, only

clusters of 20 (or greater) voxels that were significant at p=0.001 were considered as reliable brain 'activations'.

Results

We first looked at the activation of brain areas occurring while subjects watched the baseline segments of the clips, depicting an individual performing various everyday activities alone, compared to rest. The comparison of 'baseline' AR versus rest revealed the activation of a large bilateral network of brain regions encompassing visual areas, both primary and higher order, auditory areas, superior and anterolateral temporal cortex, temporal pole, superior parietal cortex, dorsal and ventral premotor cortex (including pars opercularis and triangularis), medial prefrontal (BA 9/10) cortex, orbitofrontal cortex, head of the caudate, thalamus and amygdala. A substantially identical map of activated brain areas was also observed in the comparison of 'baseline' segments of CS clips versus rest. Figure 1 shows the map of 'baseline' CS versus rest.

Insert Figure 1 about here

The comparison of the 'relational' segment of the AR clips versus rest revealed a bilateral network of activated areas very similar to the network activated for observation of the 'baseline' versus rest. The only differences were that the orbitofrontal cortex, the superior parietal cortex and the caudate failed to reach significance. Additionally, activation of the precuneus was present while viewing the AR 'relational' segments. A substantially identical map was also observed for the comparisons of the 'relational' segment of the CS clip versus rest. Figure 2 shows the map of the CS 'relational' segment versus rest.

Insert Figure 2 about here

The comparison of the AR and CS 'relational' interaction segments versus the corresponding 'baseline' segments revealed similar networks of activated areas, although the activations were more robust for the AR 'relational' segments minus 'baseline'. For both types of relationships, the following brain regions were more active during the 'relational' segments than the 'baseline' segments of the clip: extrastriate cortex, superior temporal and anterior temporal cortex, temporal pole, dorsal and ventral premotor areas (including pars opercularis and triangularis), medial prefrontal cortex (BA 9/10), precuneus, and amygdala (Figure 3 and 4).

Insert Figure 3 and 4 about here

Finally, the comparison between the 'relational' segments of AR and CS clips revealed that only AR relationships yielded additional activations compared to CS relationships. These activations were located bilaterally in the temporal poles and anterolateral temporal cortex, in Broca's and Wernicke's area in the left hemisphere, in the right insula, and in medial prefrontal and posterior cingulate cortex, as shown in Figures 5.

Insert Figure 5 about here

Discussion

The data presented here have two striking features. First, brain regions that are typically activated in the kinds of cognitive tasks that cognitive neuroscientists have usually asked subjects to perform in the laboratory did not seem to respond to the presentation of the naturalistic social stimuli that were used in our experiment. The dorsolateral prefrontal cortex, often associated with reasoning, monitoring and control; the anterior cingulate cortex, also associated with monitoring and control; and the lateral aspect of the posterior parietal cortex, often engaged in attentional tasks,[4] are not activated by the observation of the movie clips. The lack of activation in these brain areas, in

the presence of very strong activations in several other brain regions, suggests that the processing of social stimuli does not require a strong engagement of reasoning, monitoring, control, and attention. This seems compatible with a view of social cognition in which automaticity plays an important role.[24, 25, 44] [8, 9] Indeed, for humans social relationships are ubiquitous and must be processed constantly. Indeed, relational cognition is so adaptively important that humans are likely to have evolved reliable automatic mechanisms for recognizing basic types of relationships.[10]

The second unexpected feature of our results is that the observation of a single person or of two persons interacting yielded a substantially similar network of activated areas. The only brain area activated during the observation of the 'relational' segment but not during the observation of the 'baseline' segment of the clip was the precuneus. The precuneus is a region receiving strong visual input and sending robust projections to frontal areas of premotor significance. In the macaque, regions homologous to the precuneus in the medial wall of the posterior parietal cortex have demonstrated important sensory-to-motor transformation properties.[45] In the human brain, the precuneus has been reported activated in a large variety of tasks and experimental conditions. Relevant here, activation of the precuneus has been reported in tasks that involve self-referential mental activity,[14, 15, 38] and in association with episodic memory retrieval.[4, 27, 30, 43] Also, other studies have shown that the precuneus was activated when subjects made evaluative judgments (i.e., judgments in which the person's value system is critical),[50] judgments about themselves [22], or made empathy or forgivability judgments [7]. All of these tasks probably evoke cognitive and emotional processing associated with relationships. Taken together, this evidence suggests that the precuneus activation may be related to a mechanism according to which viewing the relational segments of the clips may have induced subjects to retrieve personal knowledge of the relationship shown. A similar mechanism may account for the activation of the rostralmost part of the medial prefrontal cortex (BA9/10), a region that is also being involved in self-referential mental activity.[14, 15, 38] In contrast with the precuneus activation that occurred only for the 'relational' segments, the medial prefrontal activation occurred for both 'baseline' and 'relational' segment of the clips, although medial prefrontal activity was stronger during the 'relational' segment. The medial prefrontal

activation during 'baseline' segments may be related to mindreading processes that are often associated with this brain region[11] and that likely occurred when subjects watched either one or two persons.

Given the overlap of activations in the 'relational' and 'baseline' segments of the clips, it is tempting to conclude that relational cognition occurs even when non-relational behavior is observed. That is to say, given the importance of relational cognition,[8, 9] observations of a person may always evoke relational cognition concerning the person's existing or potential relationships: People are functionally significant to each other primarily as participants in actual and possible relationships. The Gestalt psychologists of the early twentieth century argued that anytime a stimulus is observed, it is always understood within its relational context. Similarly, Mead[31] argued that whenever we think about one's 'self', it is always in comparison to someone else or an averaged 'generalized other,' so that there is no such thing as thinking about the self in isolation. Our results suggest that this is true when perceiving others, as well: we look at them in terms of the relationships they have, or could have, with others or ourselves.

We designed our experiment so that subjects merely observed others, without having to perform any reflective analyses or make any explicit inferences. We did so to maximize the ecological validity in our study. After all, while we walk, wait in line, or attend a party, we often simply watch people interacting without explicitly reasoning about the interactions.[13] Explicit analyses and judgments about social interactions may also occur, but they seem to involve another level of cognition beyond simply making sense of a social event. A second reason for not engaging our subjects in a specific task was to maximize potential comparability with the single-unit studies in macaques that have provided so many insights into neural mechanisms for understanding social stimuli. Most of these studies are carried out without requiring the monkeys to respond overtly. Thus, with our approach we believe we preserved our ability to make more precise comparisons across species and possibly to speculate on evolutionary mechanisms that played a role in the neural systems relevant to the processing of social stimuli.

In the macaque, premotor neurons located in the inferior frontal cortex fire when the animal makes an action and when the animal observes somebody else making the same action ('mirror' neurons). This observation/execution matching system seems a parsimonious neural mechanism for understanding the actions of others. In the human brain, similar neural mechanisms have been described. Our study clearly shows bilateral activation of the inferior frontal cortex during observation of both 'baseline' and 'relational' part of the clip. The location of the activation in pars opercularis and pars triangularis of the inferior frontal gyrus match well the activation found by a recent re-analysis of 47 subjects performing hand action imitation and 58 subjects performing hand action observation that we carried out in our lab (Molnar-Szakacs et al, in preparation).). This suggests that this region is important for understanding social as well as manipulative actions. That is, there is evidence here for a common neural system for representing actions, regardless of the agent performing them.

It has been objected that a possible confound, in our studies as well as in previous research, is that observation of action may elicit some internal speech, thus activating areas, such as pars opercularis and triangularis, that are known to be important for language. In our study, in fact, one need not invoke internal speech to account for inferior frontal cortex activation, given that in most of our clips the characters speak aloud. Although we believe that language processing can partly account for the inferior frontal activation, there are two reasons to explain the inferior frontal activity as reflecting a premotor system critical to the matching of observation and execution of actions. First, the activation in inferior frontal cortex is clearly bilateral, whereas language tasks tend to show activations that are stronger in the left hemisphere, if not entirely confined to it. Second, a critical role of pars opercularis in imitation (a behavior that requires the processing of actions of others) has been recently provided by a repetitive transcranial magnetic stimulation study performed in our lab. In this study, a 'virtual lesion' of pars opercularis produced a deficit in imitation but no deficit in a visuomotor control task that did not involve processing of observed actions (Heiser et al, in preparation).

Single-unit studies have reported that neurons in the superior temporal sulcus of the macaque brain respond to socially meaningful stimuli, such as hand-object interactions, gaze direction, head orientation, and faces.[34-36] Similar results were obtained by imaging studies in humans.[2, 17, 37] In terms of anatomical location, however, the recordings of single cells in the macaque and the activations observed in imaging studies in humans do not precisely correspond. Single-unit studies were typically performed in relatively anterior sectors of the superior temporal sulcus, whereas the activations observed in human studies were often observed in the most posterior sector of the superior temporal sulcus, typically where the sulcus divides in its two branches, the sulcus horizontalis and the sulcus angularis. One possible explanation for this discrepancy would be evolutionary changes in the primate brain involving migration of the superior temporal neuronal ensembles that detect biologically relevant stimuli from more anterior to more posterior sectors of the sulcus. Our study, however, clearly shows well separated foci of activation along the superior temporal sulcus. Some of the foci are posterior, and compatible with previous imaging studies in humans, and some of the foci are much more anterior, compatible with the location of single-unit recordings in macaques. It must be noted that previous human imaging studies investigating biological motion have typically used stimuli composed of simple body part movements not embedded in a rich social context. The posterior sectors of the superior temporal cortex are well connected with the parietal cortex,[41] while and the anterior sectors of the sulcus are well connected with the frontal cortex.[3] Hence one would be tempted to conclude that the activation foci along the superior temporal sulcus observed in our study reflect two different kinds of biological motion processing. The posterior ones, influenced by parietal kinesthetic processing, may be relevant to a detailed description of motor parameters of the observed actions. In contrast, the anterior temporal foci, influenced by the integrative role of frontal processing, may be relevant to the social meaning of the observed actions.

The temporal poles, mostly in the right hemisphere, exhibited strong activation whenever subjects were watching individuals alone or in interaction; there was more activity while watching the AR 'relational' segments than the CS 'relational' segments.. Temporal pole activation is not often

observed in imaging studies and the strong activations we observed may reflect the choice of ecologically valid stimuli used in our experiment. In fact, the temporal pole activation probably represents the integration of individual elements of the scene into a social context, a 'meaning'.[28] It is possible that the 'meaning' of AR clips was more salient than the 'meaning' of CS clips, hence the difference between the two. In the clips selected for this study, contextual cues may have been more important for determining AR relationships. However, these contextual cues also appear necessary for processing CS relationships, since CS clips also activated the temporal poles, as shown by Figures 1 and 2. An alternative explanation for the greater temporal pole activation while watching AR relations is that it corresponds to the additional processing involved in AR. While understanding both CS and AR relationships entails implicit analysis of whether the observed persons differ or are the same—in status or group membership - understanding AR requires implicit analysis of the direction of the difference: who is superior.

The greater posterior cingulate activation while watching AR relations may be associated with the role of this structure in affective processing [26, 29]. Although both positively and negatively valenced clips were present for both types of interaction, the AR clips were judged as somewhat more negative during pretesting. In fact, nearly half the AR clips depict a correction, rebuke, or minor transgression, or imply that the superior person is judging the subordinate. None of the CS clips depict any kind of relational tension or problem. Also, a slight unbalance in language use, with greater language use in AR 'relational' segments may also account for the activation of Broca's and Wernicke's areas in the direct comparison between AR and CS relationships.

Given the increasing evidence of cerebellar involvement in complex behavior, one might be surprised to see small cerebellar activations in our study. However, this relatively negative finding (some cerebellar activations can be observed, especially in the sagittal view offered in Figure 4) may be simply due to the fact that a minority of the subjects progressively moved during the scanning sessions. Motion correction re-aligned the brain volumes of these subjects, but in two of them the cerebellum was substantially left outside the field of view. Thus, from our data it cannot be

concluded that the cerebellum is not largely activated by the presentation of the social stimuli we used.

To conclude, we can summarize the results of our study as follows. First, there seems to be an overall organizational pattern of brain activity when processing social stimuli and social interactions that is quite different from the pattern of brain activity typically observed in non-social 'cognitive' laboratory tasks. Second, the understanding of human relations seems to involve the representation of actions (superior temporal and inferior frontal cortex) and of the context in which the observed actions are embedded (temporal poles). Third, it seems that we map the observed actions embedded in a social context onto our own relational knowledge, drawing on retrieval of episodes in our own experience (precuneus).

Acknowledgments

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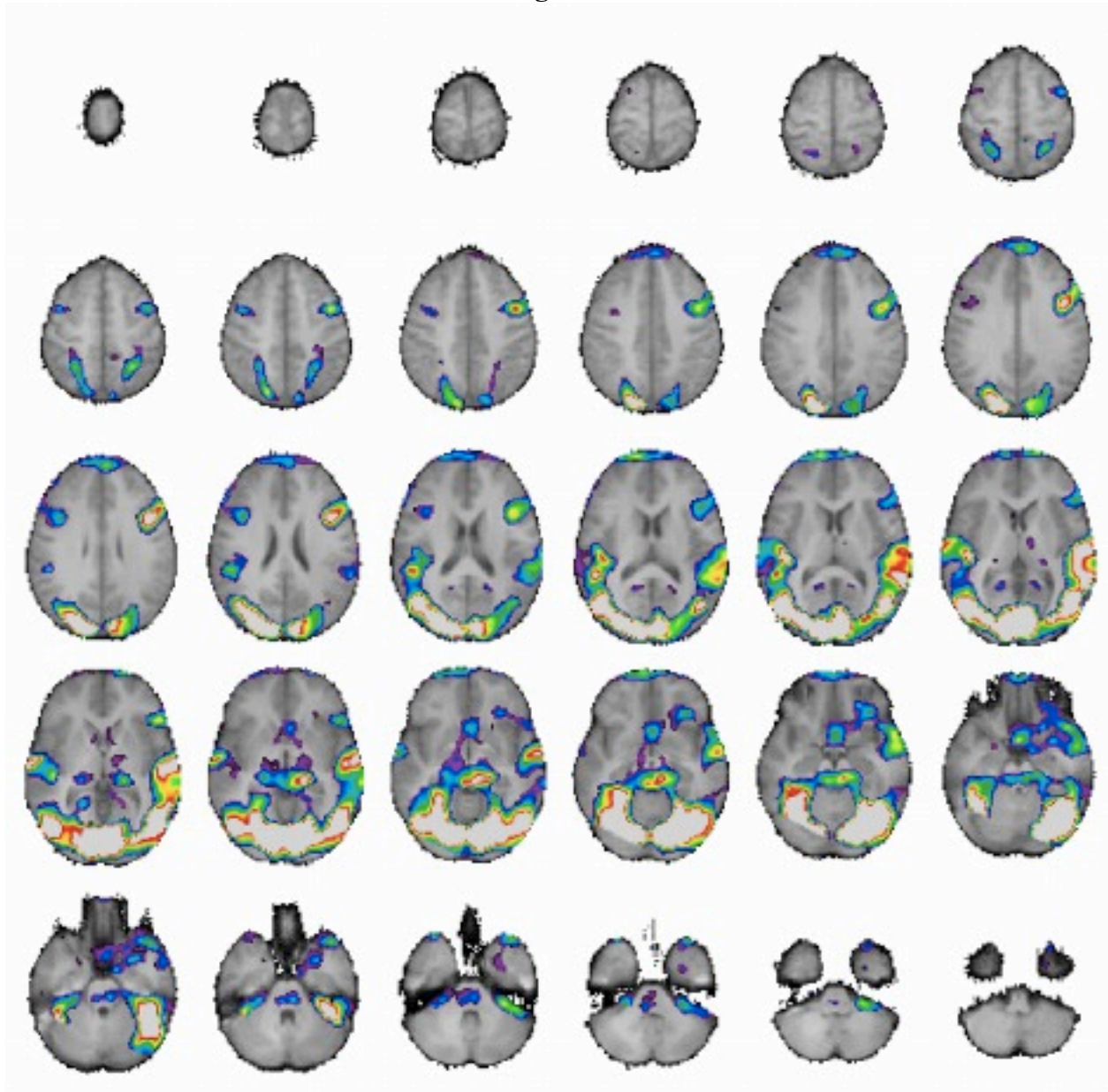
Figure 1

Figure Legend. Transverse view of statistically significant signal increases from rest to viewing the 'baseline' segment of CS clips. Color coding goes from white for maximal signal increases to purple for significant signal increases with lowest magnitude.
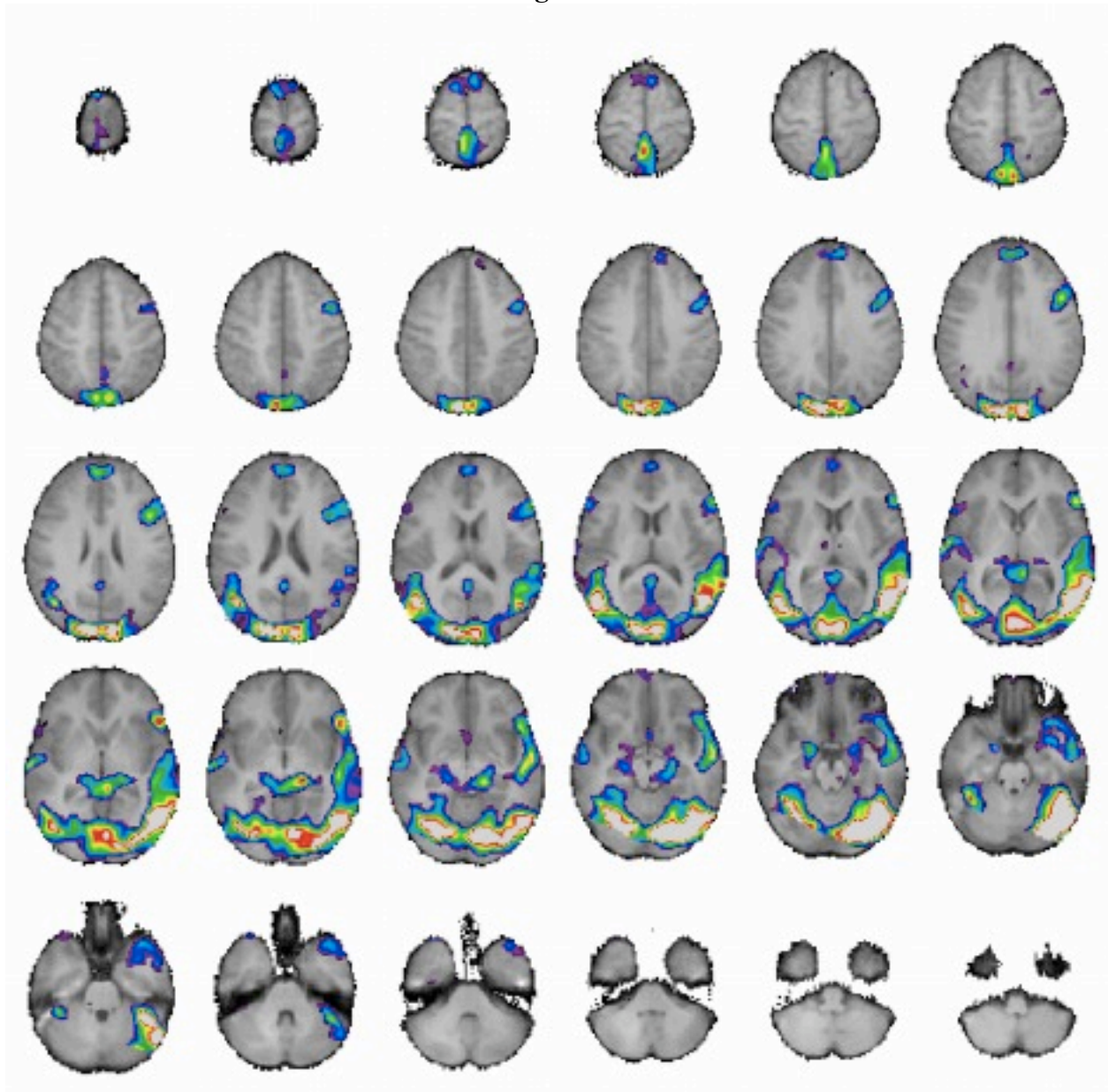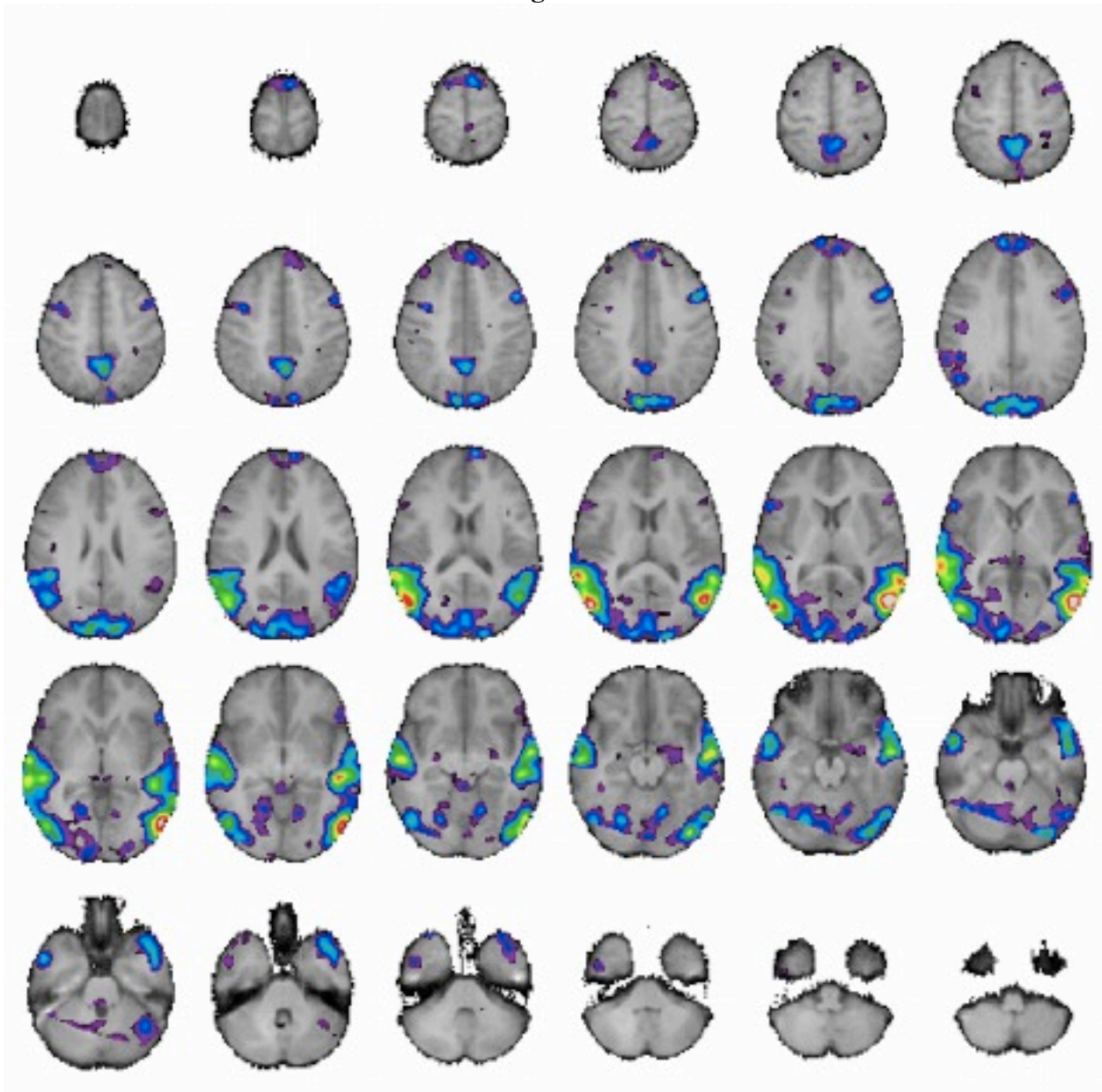
Figure 2

Figure Legend. Transverse view of statistically significant signal increases from rest to viewing the 'relational' segment of CS clips. Color coding is as in Figure 1.

Figure 3

Figure Legend. Transverse view of statistically significant signal increases from 'baseline' to 'relational' segment of AR clips. Color coding is as in Figure 1.
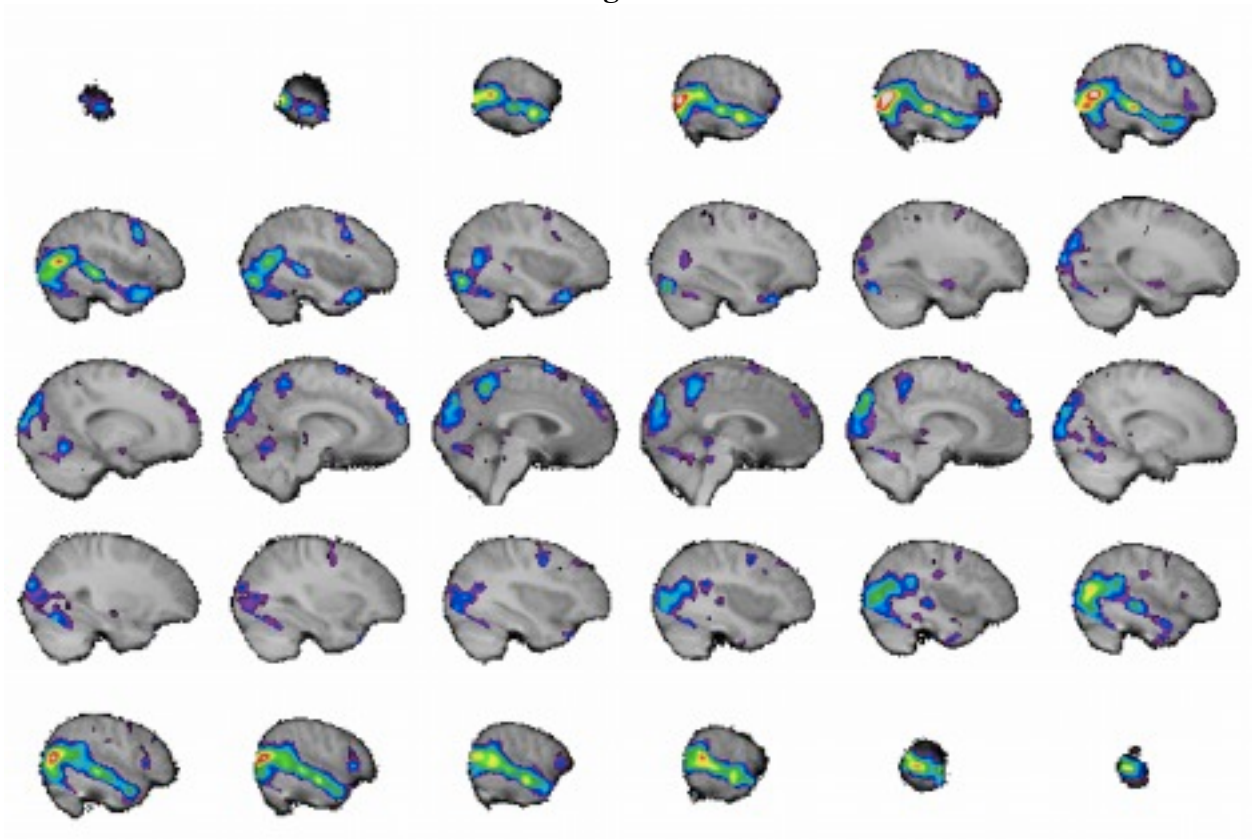
Figure 4

Figure Legend. Sagittal view of statistically significant signal increases from 'baseline' to 'relational' segment of AR clips. Color coding is as in Figure 1.
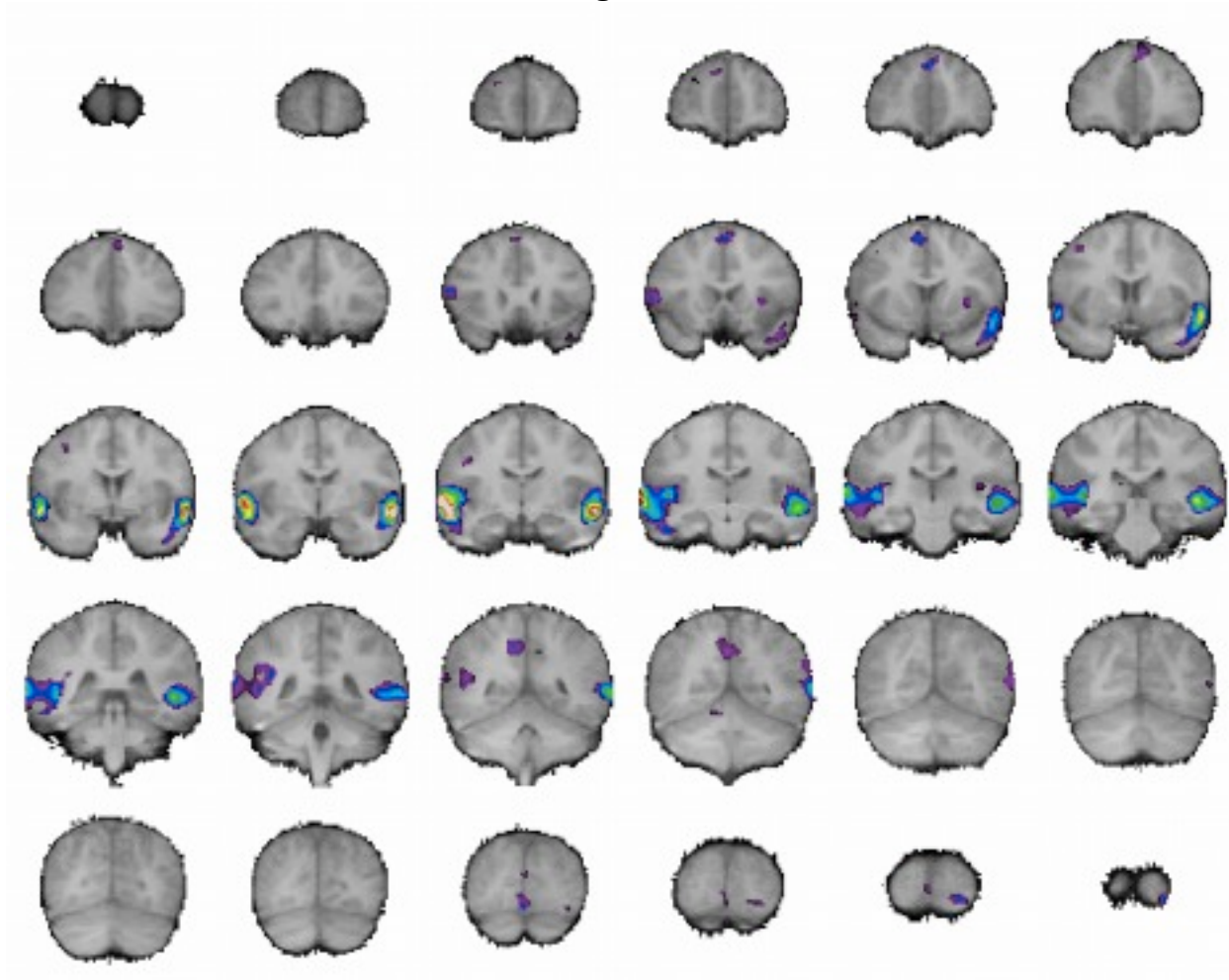
Figure 5

Figure Legend. Coronal view of statistically significant signal increases from viewing the 'relational' segment of CS clips to viewing the 'relational' segment of AR clips. Color coding is as in Figure 1.