Correction

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Correction for "Functional evolution of new and expanded attention networks in humans," by Gaurav H. Patel, Danica Yang, Emery C. Jamerson, Lawrence H. Snyder, Maurizio Corbetta, and Vincent P. Ferrera, which appeared in issue 30, July 28, 2015, of *Proc Natl Acad Sci USA* (112:9454–9459; first published July 13, 2015; 10.1073/pnas.1420395112).

The authors note that a number of the references in the manuscript and supporting information appeared incorrectly. On page 9455, left column, first full paragraph, line 11, "(17)" should instead appear as "(15)." On page 9459, left column, first paragraph, line 2, "(64)" should instead appear as "(58)." On page 1 of the supporting information, left column, second full paragraph, line 8, "(65)" should instead appear as "(59)." On the same page, right column, first full paragraph, line 3, "(66)" should instead appear as "(60)." On the same page, right column, second full paragraph, line 5, "(67)" should instead appear as "(61)." In the same paragraph, line 11, "(68)" should instead appear as "(62)." In the same paragraph, line 15, "(69)" should instead appear as "(63)." On the same page, right column, fourth full paragraph, line 7, "(70)" should instead appear as "(64)." On page 2 of the SI, left column, second full paragraph, line 17, "ref. 70" should instead appear as "ref. 64." On the same page, right column, first paragraph, line 5, "(71)" should instead appear as "(65)." On the same page, right column, first full paragraph, line 15, "(71)" should instead appear as "(65)." On page 4 of the SI, left column, third full paragraph, line 4, "(64)" should instead appear as "(58)." On page 7 of the SI, in the legend for Fig. S2, line 2, "ref. 72" should instead appear as "ref. 66." The online version has been corrected.

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Functional evolution of new and expanded attention networks in humans

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Macaques are often used as a model system for invasive investigations of the neural substrates of cognition. However, 25 million years of evolution separate humans and macaques from their last common ancestor, and this has likely substantially impacted the function of the cortical networks underlying cognitive processes, such as attention. We examined the homology of frontoparietal networks underlying attention by comparing functional MRI data from macaques and humans performing the same visual search task. Although there are broad similarities, we found fundamental differences between the species. First, humans have more dorsal attention network areas than macaques, indicating that in the course of evolution the human attention system has expanded compared with macaques. Second, potentially homologous areas in the dorsal attention network have markedly different biases toward representing the contralateral hemifield, indicating that the underlying neural architecture of these areas may differ in the most basic of properties, such as receptive field distribution. Third, despite clear evidence of the temporoparietal junction node of the ventral attention network in humans as elicited by this visual search task, we did not find functional evidence of a temporoparietal junction in macaques. None of these differences were the result of differences in training, experimental power, or anatomical variability between the two species. The results of this study indicate that macaque data should be applied to human models of cognition cautiously, and demonstrate how evolution may shape cortical networks.

attention | human | monkey | fMRI | cortex

Selective attention operates in at least two functional modes: stimulus-driven (bottom-up) control of attention and goal-directed (top-down) (1). A recently proposed model by Corbetta et al., based on human neuroimaging and stroke studies, divides the control of attention between two cortical networks that underlie these modes of attention: the dorsal attention network, comprising the human frontal eye-fields (FEF) and intraparietal sulcus (IPS), and the ventral attention network, centered around an area at the temporoparietal junction (TPJ), located on the right hemisphere caudal supramarginal gyrus (Brodmann area 40 or area PFG/PF) and posterior superior temporal gyrus (Brodmann area 22) (2–4). This functionally defined ventral attention network area is referred to as the TPJ by Corbetta et al. (2) and TPJa in Mars et al. (5). Here, we refer to the functionally defined area as the TPJ, and reserve "temporoparietal junction" for the anatomical region in both species. According to this model, the dorsal attention network is activated when the subject sustains attention on a cued spatial location (6). The TPJ is activated only by the presentation of a behaviorally relevant stimulus that captures attention, with larger activations evoked by stimuli that are unexpected or cause reorienting of attention, and is deactivated when distracting stimuli are presented during sustained attention (6, 7). The conjunction of deactivation during sustained attention and activation during target detection functionally identifies the TPJ in event-related paradigms (6). Damage to the TPJ decreases the ability to detect and orient attention to novel stimuli presented, especially in the left hemifield, a condition known as visuospatial neglect (3). The dorsal and ventral attention networks interact with each other and with the visual cortex (2). During top-down or goal-directed control of attention, the dorsal attention network is activated, enhancing the selected stimulus in visual cortex, and the TPJ is deactivated, suppressing the orienting of attention to potentially distracting stimuli. However, when a behaviorally relevant stimulus is presented, the TPJ is activated, causing attention to be focused on this stimulus (2). However, these roles of the TPJ in the control of attention remain open to debate, partly because little is known about the TPJ's connectivity or neuronal response properties.

The macaque has been used as a model for studying attention using invasive techniques that complement neuroimaging. There are established maps of cortico-cortical connectivity (8) and many electrophysiological studies of how these areas interact (9). As with all model systems, interspecies differences in these cortical systems are likely to exist. For example, the dorsal attention networks are assumed to be homologous between the two species, but basic facts, such as the number of areas within the dorsal network in each species, remain unknown. Furthermore, a ventral attention system has been functionally characterized only in humans, and the underlying architectonics and connections remain largely unknown. The macaque model might be used to examine these features, but in macaques the ventral attention system has not been functionally isolated and an anatomical homolog is unclear. Areas PF/7b or PFG seem most likely to be anatomically homologous to the human TPJ, but functionally these areas are more involved in polysensory

Significance

Macaque monkeys are often used as a model for the biological basis of human cognition. However, the two species last shared a common ancestor 25 million years ago, and in the intervening time the brain areas underlying cognition have likely evolved along different paths. We examined the similarities and differences of human and macaque brain areas underlying attention, a core cognitive ability, by recording brain activity while subjects of both species performed the same attention-demanding task. We found fundamental differences in the attention-related brain areas in the two species, including the complete absence, in monkeys, of a ventral-attention network present in humans. These results shed light on the evolution of the unique properties of the human brain.

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integration and motor functions than in the control of attention (4, 10, 11). A recent functional connectivity study (12) found an area in the region of the macaque temporoparietal junction that shares a similar pattern of connectivity and right hemisphere lateralization with the human TPJ. However, this potential homolog covers multiple areas—7a, temporal parietal occipital caudal, and retroinsular—with no unifying function (13). However, another recent study finds the homolog of a human area adjacent to the TPJ involved in social cognition to be located in the mid-superior temporal sulcus of the macaque, far from the expected location at the macaque temporoparietal junction (14). Many details about the anatomy and physiology of the ventral attention network in either species remain unknown (3, 5).

To address the similarity of attention systems, we quantitatively compared humans and macaques using functional MRI (fMRI). We had both species attend to and search through a rapid serial visual presentation (RSVP) stream of images to detect a previously memorized target image. The task was designed to separate activation of visual areas and the dorsal attention network from deactivations of the TPJ during search (which combines sustained covert attention and visual processing of the RSVP stimuli), and activation of the TPJ by target detection (Fig. S1*A*) (2, 6). We used the same macaque data to report on topographic organization in the lateral intraparietal (LIP) previously (15).

Results

Behavior. Behavior in humans and macaques was closely matched. Fig. S1*B* shows that the range of detection rates in the eight human subjects approximated that of the two macaques. Although a button-box malfunction made the recorded reaction times for the humans in the MRI scanner unusable, the human reaction times recorded in the behavioral set-up (human mean 0.541 s, SD = 0.036) were similar to the macaque reaction times (macaque Y mean 0.539 s, SD = 0.062; macaque Z 0.484 s, SD = 0.048) (Fig. S1*C*). Fixation breaks in the human subjects were relatively infrequent (0.247 fixation breaks per trial, SD = 0.170) and relatively short (0.508 s per fixation break, SD = 0.080), and the average fixation position in humans was similar to the macaques (Fig. S1*D*).

Topography of Activation Maps. Qualitatively, the patterns of activation in both species showed broadly similar patterns but several clear differences. The two-stream trials in both species evoked activations in the visual cortex as well as attention-related areas of the parietal and frontal cortex. For each individual, we defined cortical surface frontoparietal regions of interest (ROIs) as contiguous activations that were consistent in most individual's hemispheres ($P < 0.05$ Bonferroni multiple comparisons correction). These were then labeled by comparing locations to previous functional and anatomical studies in each species (see *SI Materials and Methods* for more details). This qualitative analysis revealed activation patterns that were highly consistent within species but markedly different between species (Fig. 1 and Figs. S2–S4). In the parietal lobe of all four monkey hemispheres there was only one focus of activity on the lateral bank of the IPS corresponding to the anatomical location of area LIP (Fig. 1 *A* and *C*). One additional focus of activity may have been present corresponding to area dorsal prelunate, but was not consistent and may have been V2/3d activity misprojected to the opposing sulcal bank. Similarly, Fig. 1*C* demonstrates that the activity on the medial bank of the IPS in Fig. 1*B* represents misprojection from the lateral bank. In most of the humans, however, two parietal foci were identified (Fig. 1*B*), one in the ventral portion of the IPS (vIPS, 13 of 16 hemispheres) and one in the posterior portion of the IPS (pIPS, 16 of 16 hemispheres). In the macaque prefrontal cortex, two adjacent foci were consistently identified in the four hemispheres: one on the anterior bank of the arcuate sulcus corresponding to the anatomical location of the FEF, and the other at the posterior end of the principal sulcus (area 46). Fig. 1 *A* and *C* also demonstrate potential foci in the inferior and posterior ramus of the arcuate sulcus, but neither of these were consistently present in all four hemispheres and did not match known oculomotor or attention areas in the macaque; these foci were not considered further. In the human prefrontal cortex, three foci were consistently identified (Fig. 1*B*): one at the junction of the precentral and superior frontal sulcus corresponding anatomically to what has been previously labeled as the FEF (14 of 16 hemispheres), one inferior to this location in the precentral sulcus (iPCS, 14 of 16 hemispheres), and another in the anterior portion in or near the inferior frontal sulcus (aIFS, 12 of 16 hemispheres). These gross qualitative differences in the functional anatomy of the dorsal attention network are reinforced by the quantitative measurements of areal characteristics described below.

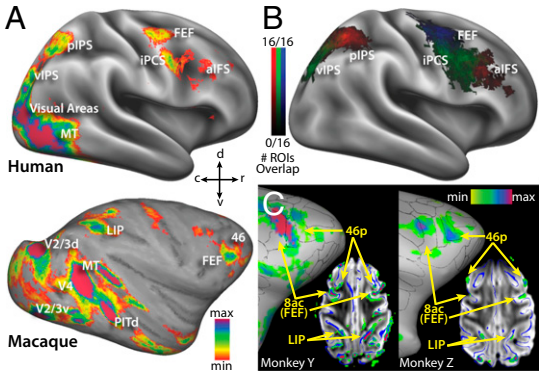

Fig. 1. (*A*) Areas activated by two-stream paradigm averaged across both hemispheres for all subjects of each species. Human labels derived from sulcal features, and macaque labels derived from ref. 13. Threshold set at $z > 10$ for both species ($P << 0.05$ multiple comparisons corrected). Human data on the Conte 69 right hemisphere cortical surface, and macaque data on the macaque F6 right hemisphere surface. (*B*) Overlap of human areas activated in the two-stream paradigm from all 16 hemispheres. Locations with more overlap have lighter shades of color. (*C*) Two-stream activations in both individual macaques, overlaid on their own epipolar plane image (EPI) volumes and cortical surface models ($P < 0.05$ multiple comparisons corrected). Blue lines on EPI volumes represent cortical surface outline. Black lines on surfaces represent architectonic borders in ref. 13, in which, area 8ac partially overlaps the functionally defined FEF, and area 46 is subdivided into 46p and 46v.

Contralateral Preference. For each subject, the foci from the two-stream data described above were used to create ROIs, from which were extracted time courses of blood-oxygen level-dependent (BOLD) activity evoked by the 12-s RSVP stream presentation for each of the six locations at 6.8° eccentricity. For each ROI, the average magnitude of activation was calculated for the three contralaterally and ipsilaterally presented streams over the peak activation period (3–12 s for the macaques and 6–15 s for the humans) (Fig. 2*A*). The contralateral and ipsilateral magnitudes were then used to calculate a contralaterality index [(contra − ipsi)/contra], with values of 1 indicating no evoked ipsilateral activity and 0 indicating equal contralateral- and ipsilateral-evoked activity (Fig. 2*B*). In both species, visual cortex ROIs [V1, V2/3v, V2/3d, V4, middle temporal (MT)] had contralateral index values near 1, indicating little or no ipsilateral-evoked activity in these areas. In macaques, frontoparietal areas were also strongly lateralized, with index values near 1 [repeated-measures ANOVA, hemisphere × ROI, ROI: $F_{(7,7)} = 1.57$, $P = 0.429$]. However, in humans, the contralateral bias of the frontoparietal areas was significantly decreased [repeated-measures ANOVA, hemisphere × ROI, ROI: $F_{(9,63)} = 25.9$, $P < 10^{-15}$]. There was no significant effect of hemisphere on the contralateral preference in humans [hemisphere: $F_{(1,7)} = 0.15$, $P = 0.71$].

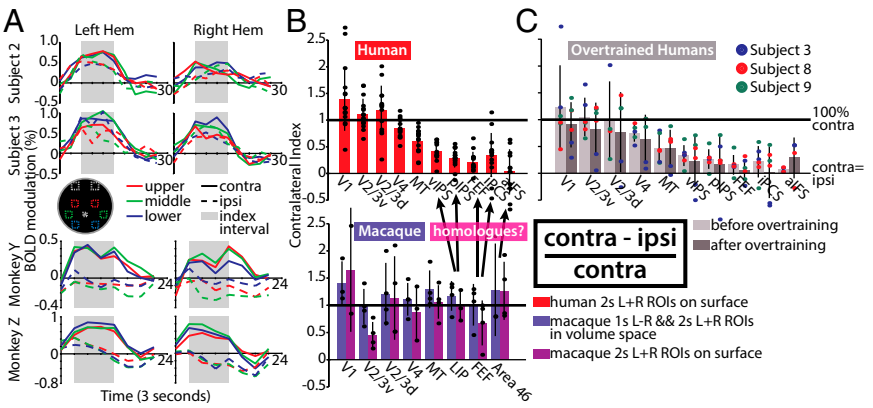

Fig. 2. (*A*) Time courses of contralaterally evoked versus ipsilaterally evoked activity in the parietal cortex (macaque LIP and human pIPS). (*B*) Contralateral preferences in humans and monkeys. Bars represent mean preference of all hemispheres, error bars SD, and each black dot a measurement from one hemisphere of one subject. Index value of 1 represents complete contralateral bias (no ipsilaterally evoked activity) and 0 equal magnitudes of contralaterally and ipsilaterally evoked activity. (*C*) Effect of overtraining on human contralateral preferences in three subjects.

To determine whether the contralateral index differences in the two species were a result of differences in training history, three of the human subjects trained for an additional ~19 h over 3–4 mo on the single-stream task, and were then scanned once again while performing that task. Using the same ROIs as in the pretraining session, contralateral index values were recalculated from the posttraining scanning session (Fig. 2*C*). On average, the contralateral index did not change significantly with training [repeated-measures ANOVA, pre/posttraining × hemisphere × ROI, main effect of training: $F_{(1,2)} = 0.144$, $P = 0.741$]. In fact, in 9 of 10 regions the average degree of contralateral preference decreased with training.

Functional Localization of the TPJ. In humans, the TPJ node of the ventral attention system was defined on the group average map on the Conte 69 surface as voxels on or near the right hemisphere supramarginal gyrus that were both significantly deactivated while searching for targets and significantly activated by the detection of targets (Fig. 3). This resulted in an ROI with similar shape and location as defined in Shulman et al. (6); a comparison of Fig. 3 with Fig. S5 demonstrates the hemispheric asymmetry in the TPJ seen in Shulman et al. and other studies (6, 7, 12). In macaques, the same conjunction failed to reveal any similar ROI on or around the inferior parietal lobule or superior temporal gyrus in either hemisphere at the group level (Fig. 3*A*).

To verify that the group average human TPJ ROI reliably represented the TPJ in each individual, this ROI was projected to each individual's surface and used to extract time courses of BOLD activity. These time courses revealed substantial deactivation evoked by visual search and activation evoked by target detection in all eight subjects (Fig. 4*A*). Because no similar ROI could be defined in the macaques, the human surface ROI was projected to the macaque atlas surface using the interspecies registration algorithm in CARET (www.nitrc.org/projects/caret). The projected ROI overlapped with macaques areas 7op and PA in the Lewis and van Essen atlas (13). This surface ROI was then used to extract BOLD time courses of activity for visual search and detection using the same procedure in macaques and humans. These time courses did not reliably reveal either search deactivations or target activations in any of the four macaque hemispheres, with the exception of one left hemisphere deactivation; this is in contrast to finding search deactivations and detection activations in all human subjects. In the three subjects that underwent additional training and a posttraining scan, the search deactivations and detection activations did not change substantially after training (Fig. 4*B*). A recent study used resting-state functional connectivity to isolate a potential macaque TPJ homolog (12) (Fig. 3). BOLD time courses extracted from the ROI revealed by this method, which overlaps considerably with the projected human ROI, also show neither the search activations nor detection activations that would be expected of a macaque homolog of human TPJ (Fig. S6).

Discussion

We compared BOLD-fMRI responses of the attention and visual systems of eight humans and two macaques using identical tasks, and found three consistent differences between species. First, although dorsal frontoparietal regions were activated in both species, in monkeys there were fewer independent activation foci in both the parietal and prefrontal cortex. Second, both species demonstrate contralateral bias in visual and dorsal frontoparietal regions, but the bias is much weaker in the human frontoparietal cortex. Finally, we found no evidence of an area in macaques located in the temporoparietal region having the functional properties of human TPJ (as measured by our task), despite robust and consistent modulation of activity of the TPJ in humans with the same task. All results were highly consistent within species and highly divergent between species. They likely do not reflect a verbalization strategy in humans, as left hemisphere language areas were not activated (*SI Discussion* and Fig. S2). The results also cannot be attributed to differences in performance, training, or reward structure (Fig. S7), and therefore

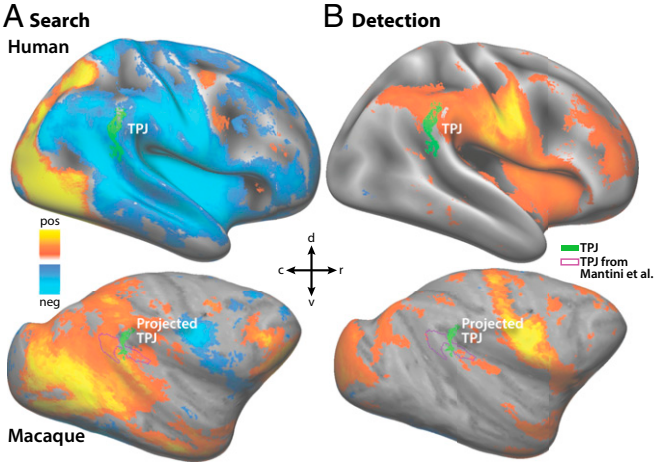

Fig. 3. Activations/deactivation evoked by search and detection. Fixed-effects group average maps of right hemisphere cortical voxels activated and deactivated while (*A*) searching for or (*B*) detecting a target in the one-stream paradigm. Threshold set at $P < 0.05$ multiple comparisons corrected [$z > 4.9$ for humans (*Upper*) and $z > 4.7$ for macaques (*Lower*)]. The green is the TPJ region of interest formed by the conjunction of the underlying search deactivations in *A* and detection activations in *B* on the right supramarginal gyrus in humans and projected to macaques.

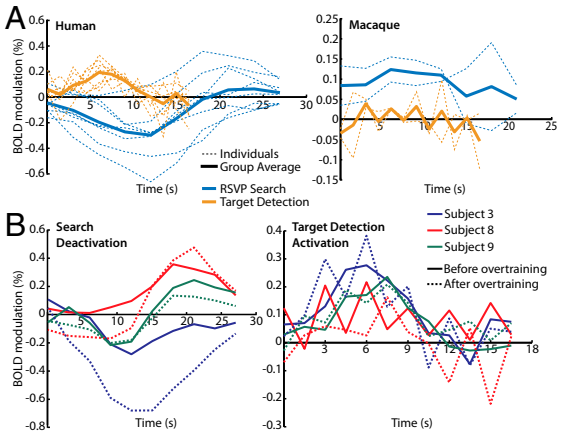

Fig. 4. (*A*) Time courses of TPJ transient activations evoked by target detection (orange) and sustained deactivations evoked by 12 s of search (blue), both realigned to start at 0 s. Human time courses derived from conjunction ROI shown in Fig. 3, and macaque time courses derived from projected ROI shown in Fig. 3. (*B*) Time courses of sustained search deactivations and transient target detection activations from TPJ before (solid lines) and after (dotted lines) training sessions.

likely reflect species differences that have evolved in the 25 million years since the most recent common ancestor (18).

Expansion of the Dorsal Attention System in Humans. These evolutionary changes result in fundamental differences in the architecture of the attention systems. Even in the dorsal attention system, which is broadly similar in the two species, a property as basic as the number of areas involved in a visual search task differs between species. Although the macaque cortical sheet is about 10× smaller in area than humans and about 1-mm thinner (19), the 8× finer fMRI sampling resolution in macaques (1.5-mm isotropic) compared with humans (3-mm isotropic) was sufficient to resolve foci from adjacent cortical areas, which are typically several millimeters in width and length (further discussed in *SI Discussion*). In addition, despite individual variation, and even with the small number of subjects, there was a remarkable degree of consistency within species. The main conclusions of this study are consistent with those of previous human imaging studies (20–23) and macaque anatomy and electrophysiology (9, 13, 24).

Two previous oculomotor studies comparing macaques and humans using BOLD-fMRI also found more individual foci of activity in humans than in macaques (25, 26). The sustained working memory task in Kagan et al. (25) is comparable to our covert attention and search task. That study, like ours, found a single parietal focus of activation in macaques versus multiple foci in humans. The macaque activation was in the anatomically and functionally defined LIP (13, 27), whereas the human activations were along the IPS on the superior parietal lobule (pIPS in our study) and in the ventral IPS (vIPS in our study), in keeping with other studies (2). The pIPS in our study has been previously labeled human LIP (20) based on topographic organization, but recent studies in humans and macaques have found that there may be more parietal areas along the IPS in humans than macaques (23), and that topographic organization in the macaque LIP may be more complex than previously thought (27), making it difficult to identify parietal area homologies in the two species.

In the macaque frontal cortex, we, in agreement with both Koyama et al. (26) and Kagan et al. (25), find two foci of activity: one in the anterior bank of the arcuate sulcus, corresponding to the FEF (28), and one in the posterior portion of the principal sulcus, corresponding to posterior area 46 (29). This finding is in contrast to the three foci of activity typically observed in the human frontal cortex (21–23). The most anterior of these three—the aIFS—is likely homologous to macaque area 46 (29). It is unclear the degree to which the two remaining foci of activity—which we labeled FEF and iPCS—are homologous to the macaque FEF. Both Koyama et al. (26) and Kagan et al. (25), along with multiple human fMRI studies (23), have found that these two areas are activated in attention, oculomotor, and spatial working memory tasks. However, usually only the superior of these two areas is labeled as the human FEF (2, 22, 23), despite this and other inconsistencies between the two species (30). The functional differences between the human FEF and iPCS also remain unclear. Amiez and Petrides described a premotor eye-field in humans ventral to the area we have labeled the FEF, but iPCS in our study was more inferior than their proposed premotor eye-fields, which in our task were not consistently activated in macaques (31). Jerde and Curtis recently found that the FEF (sPCS in their study) exhibited more sustained activity than iPCS during oculomotor, attention, and spatial working memory tasks (21); in the context of our results, this finding suggests that the iPCS has evolved as a prefrontal cortical area in humans, but is not present in macaques. Although the expansion of the functionally defined dorsal attention network in humans versus macaques will require confirmation by comparative connectional anatomy studies, the findings appear to reflect the evolution of new or enhanced attentional abilities—possibly as a result of different evolutionary pressures—further evidence of which is discussed below.

Differences in Contralateral Preference Reflect Separate Evolution of Human and Macaque Attention Systems. Differences in the contralateral preference of the dorsal attention network provide further evidence of divergent evolution. These results corroborate previous human/macaque fMRI studies of the oculomotor system (25, 26). In the present study we show that the contralateral preference diverges between humans and macaques as one ascends the visual hierarchy into the attention system (22, 32). The divergence is most pronounced in those regions that have most expanded in humans compared with macaques over the course of evolution (33). These regions include the superior parietal and dorsolateral prefrontal cortex, perhaps indicating that selective pressures on the two species resulted in different organizational schemes (34).

The interspecies differences in contralateral preference may reflect changes in the magnocellular pathway that have been noted at multiple levels of visual processing (16). The evolution of the magnocellular pathway may underlie changes in the distribution and size of receptive fields (resulting from differences in lower-level visual input) and differences in the sharing of information between dorsal frontoparietal areas and other higher-level areas. Single-unit recording studies in the macaque find that neurons in frontoparietal attention areas have large receptive fields, and that ∼10–45% of cells have ipsilateral receptive fields (28, 35–38) as well as summation of signals from both hemifields (39, 40). In humans, both of these properties may have been extended. Studies of M (parasol) retinal ganglion cell dendritic fields and perceptive field sizes (thought to reflect M retinal ganglion cell receptive field sizes) have found both to be larger in humans than macaques (16, 17). Given that receptive field size tends to increase at each level of visual processing (41), it is possible that receptive field sizes in the frontoparietal cortex are also larger in humans versus macaques.

In humans the mechanisms for sharing signals between hemispheres and hemifields may have been elaborated in the service of brain lateralization (25), as well as improved flexibility in the use of information from both hemispheres in the control of attention (32). In macaques, selective pressures may have killed sharing of information between hemispheres in favor of faster processing (42). Increased interhemisphere information sharing in humans may

underlie the global precedence when processing complex stimuli with both global and local features, whereas in monkeys local features have precedence (16, 43). The global precedence suggests that sharing of information between hemifields is automatic in humans.

The seeming contradiction between macaque single-unit studies showing a significant proportion of cells with ipsilateral fields and macaque BOLD-fMRI from this study and from Kagan et al. (25), showing strong contralateral preferences, may reflect an unequal distribution of receptive fields within frontoparietal areas representing the contralateral and ipsilateral hemifields. In the single-unit studies, many of the receptive fields classified as ipsilateral tend to be along the vertical meridian (37) (Fig. 3), meaning that most receptive field locations are centered in the contralateral hemifield (but see ref. 44). In our study the stimuli were located 4.8–6.8° away from the vertical meridian and likely stimulated few ipsilateral receptive fields in any of the frontoparietal areas. Studies using a combination of single-unit recording and BOLD-fMRI (or LFP recording) in these areas will be needed to better understand these differences.

TPJ: Uniquely Human? There is some debate about how the TPJ is involved in the control of attention—whether it is involved in the shifting of attention (45) or in the evaluation of "oddball" stimuli (46)—but converging evidence from neglect studies implicate the TPJ in some aspect of attentional control (2, 3). The functional absence of the TPJ in macaques therefore represents a profound interspecies difference in the control of attention. The RSVP task used in this experiment robustly and consistently isolates the TPJ node of the ventral attention network in humans (6), and so the lack of analogous modulation in macaques is telling. The failure to produce deactivation was not because of a lack of power; robust deactivations were seen in the ventral motor cortex that were similar to the human subjects. Nor was it because of a potential difference in activity evoked by maintaining fixation; in humans the TPJ deactivations depend on attention and working memory load (47, 48) and it would be difficult to argue that the attention or working memory loads in the fixation and visual search task intervals were equivalent for macaques but not humans.

Additional support for this interspecies difference again comes from the phenomenon of global precedence in humans, which appears to require the right TPJ (49). The functional absence of the TPJ, combined with a dorsal attention system with smaller receptive fields and less interhemispheric communication, may explain the local precedence found in monkeys (16). These differences may be less surprising given how much more cortical surface area is devoted to the inferior parietal lobule at the junction of the parietal and temporal lobes in humans versus macaques, even after correcting for scale differences (33), but nevertheless indicate that the human attention systems differ substantially from macaques, and that the macaque model may be inadequate for some aspects of human vision and attention. There is evidence, however, that although the current task reveals species differences in the function of the temporoparietal junction, the underlying circuitry may have similar connectivity. Histological studies indicate that areas at or near the temporoparietal junction in macaques project to the ventro- and dorsolateral prefrontal cortex (particularly areas 7a and PFG), just as functional connectivity studies suggest that the human TPJ is connected to regions of the dorsolateral prefrontal cortex (2, 4). This temporoparietal-prefrontal cortex circuitry may be conserved in the two species, but used for different purposes. With a single synapse separating multimodal/associative temporoparietal cortex and prefrontal cortex, this circuit architecture may underlie the fast transfer of information from associative sensory areas to prefrontal working memory/task control centers. In macaques, this fast circuit could allow the animal to quickly navigate its arboreal environment (42). Neurons in area 7a, which is on the inferior parietal lobule near the temporoparietal junction and overlaps somewhat with the candidate homolog from Mantini et al. (12), play a role in the detection of new onset high-contrast stimuli outside of the focus of attention (50) as well as processing complex visual stimuli, such as optic flow patterns (51) and maze navigation (52). In humans, the ventral attention system also may be involved in navigating an environment of complex social cues rather than physical objects (53). In addition to their role in the control of attention, areas in or near the human TPJ are involved in the processing of faces (54), gaze direction (55), and in determining the intentions of others (56); these abilities are unique or enhanced in humans compared with chimpanzees and other nonhuman primates (53). Accordingly, the human TPJ is less sensitive to the types of sudden-onset, high-contrast, task-irrelevant stimuli that macaques may need to detect to escape predators or dodge obstacles, and more sensitive to the behavioral relevance of a stimulus (2), a characteristic that might be useful in social situations for picking out subtle changes in visual features, like eye-gaze direction. Differences in selective pressures may have caused this circuit to be adapted for different purposes in the two species.

Conclusions

The results of this study demonstrate that a task that clearly and consistently defines areas involved in attentional control in humans evokes a starkly different pattern of activations and deactivations in macaques. Given the similarity in task performance in the two species, these differences cannot be easily dismissed as confounded or artifactual. We have interpreted these findings in light of the Corbetta/Shulman model (2), but the observation that the task evokes patterns of activations and deactivations, both within and outside of human attention areas that differ markedly from the macaque, is independent of this model. These results suggest that the human and macaque attention systems have evolved in the service of the unique challenges facing each species, and in humans this has meant an elaboration of the attention control system to support new and unique functions that may underlie expanded social cognition abilities.

Although enough similarities exist to support continued use of macaques as a model system for humans, these fundamental differences in function demonstrate a need for a cautious application of findings from one species to the other (16). This study does not rule out the possibility of homologies not revealed by the task used here: other tasks may reveal shared functional features between the temporoparietal junction and dorsal attention areas in the two species. At a deeper level, these results demonstrate how differing selective pressures may adapt existing neural architectures, such as the TPJ, to perform novel functions. Understanding the evolutionary origin of these circuits will better constrain investigations of human cognitive systems, as well as provide insight into how exactly humans differ from other primates.

Materials and Methods

Two macaques were used in accordance with the Washington University Animal Studies Committee and the NIH *Guide for the Care and Use of Laboratory Animals* (57). Eight human subjects were recruited and provided written informed consent in accordance with the New York State Psychiatric Institute Institutional Review Board. Subjects of both species performed the same visual search task while BOLD images were acquired in a 3T scanner, with 1.5-mm isotropic voxels in the macaque and 3-mm isotropic voxels in the humans, both with a TR of 3,000 ms. The task required the subjects to maintain fixation while covertly attending to a 12-s RSVP stream of colorful images of objects presented in the periphery or at fixation in one location at a time, and to indicate with a hand response when they had detected a previously memorized target. Eye-tracking was used to ensure fixation, and both species were rewarded for fixation and correct detection with small drops of liquid. The BOLD images were corrected for motion and other artifacts through a series of automated image-processing programs, and were then analyzed with a general linear model that separated the sustained response to the RSVP stream from the transient response to target detections. The resulting *z*-statistic maps were projected to 3D representations of the subject's own cortical surface and then to the species appropriate atlas surface (CARET, www.nitrc.org/projects/caret/). Group averaging was performed on the cortical surface to make group ROIs, and human ROIs were projected to

the macaque atlas via the interspecies cortical surface deformation procedure outlined in (58). For more details, please see *SI Materials and Methods*.

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