



## Neural representations of social status hierarchy in human inferior parietal cortex

Joan Y. Chiao<sup>a,b,\*</sup>, Tokiko Harada<sup>a</sup>, Emily R. Oby<sup>b</sup>, Zhang Li<sup>a</sup>, Todd Parrish<sup>c</sup>, Donna J. Bridge<sup>a,b</sup>

<sup>a</sup> Department of Psychology, Northwestern University, United States

<sup>b</sup> Northwestern Interdepartmental Program in Neuroscience, United States

<sup>c</sup> Department of Radiology, Northwestern University Medical School, United States

### ARTICLE INFO

#### Article history:

Received 7 February 2008

Received in revised form 29 July 2008

Accepted 8 September 2008

Available online 17 October 2008

#### Keywords:

fMRI

Inferior parietal cortex

Number

Semantic distance effect

Social status hierarchy

Social comparison

Social neuroscience

### ABSTRACT

Mental representations of social status hierarchy share properties with that of numbers. Previous neuroimaging studies have shown that the neural representation of numerical magnitude lies within a network of regions within inferior parietal cortex. However the neural basis of social status hierarchy remains unknown. Using fMRI, we studied subjects while they compared social status magnitude of people, objects and symbols, as well as numerical magnitude. Both social status and number comparisons recruited bilateral intraparietal sulci. We also observed a semantic distance effect whereby neural activity within bilateral intraparietal sulci increased for semantically close relative to far numerical and social status comparisons. These results demonstrate that social status and number comparisons recruit distinct and overlapping neuronal representations within human inferior parietal cortex.

© 2008 Elsevier Ltd. All rights reserved.

Social status hierarchy is a ubiquitous principle of social organization across a wide variety of species in the animal kingdom, from ants (Wilson, 2000) and fish (Grosenick, Celement, & Fernald, 2007) to birds (Schjelderup-Jebbe, 1935; Tinbergen, 1936) and primates (Cheney & Seyfarth, 1990). Across a range of species, dominant groups and individuals within the hierarchy often have primary access to precious resources such as food, territory and mates while submissive individuals may expect protection or care from those of higher rank (Fiske, 1992). Navigation of social interactions within a status hierarchy requires that individuals express and recognize social status signals, such as visual cues or vocal calls, which communicate rank and convey expectations about appropriate social behavior given a hierarchical social context (Fiske, 1992; Wilson, 2000). Across species, spatial information is a critical component of social status communication. Ants and bees, for instance, recognize social status of their conspecifics from the physical body size (Wilson, 2000), while birds and primates infer social status from nonverbal cues (e.g., facial and body posture) that either expand or constrict body postures and subsequently alter perceived physical size as larger or smaller (Ellyson & Dovidio, 1985; Maestripieri, 1996; Tiedens & Fragale, 2003).

In addition to phylogenetically shared nonverbal behaviors, humans have a number of uniquely human ways for communicating social status. Across languages, for example, spatial metaphors (e.g., “top of the heap” and “bottom of the barrel”) and linguistic tense (e.g., formal and informal) effectively signify people, objects and environments that are high and low status (Pinker, 1997). Temporal features of social interaction can also serve as a reliable source of information about the social status of other people. High-status individuals, for example, typically receive primary access to resources (e.g., first in line; Fiske, 1992) and spend a longer time speaking relative to listening to others in a social conversation relative to low-status individuals, a phenomenon known as the visual dominance ratio (Dovidio & Ellyson, 1982). Culture also provides a set of associations about objects in the environment and their relative status or worth in society (Erk, Spitzer, Wunderlich, Galley, & Walter, 2002; Yoon, Gutchess, Feinberg, & Polk, 2006). For instance, certain objects, such as sports cars (e.g., Ferrari), are widely coveted as ‘status symbols’ (Erk et al., 2002; Yoon et al., 2006). Hence, people may infer the social status of other people by evaluating the social status of objects that they possess.

Because of the near ubiquitous presence of social hierarchy across species (Boehm, 1999) and cultures (Sidanius & Pratto, 2001) as well as the adaptive benefits of accurate social status inference, it is plausible that the human ability to successfully navigate hierarchical social interaction arises from adaptive mechanisms in the mind (Pinker, 1997) and brain (Allison, Puce, & McCarthy, 2000; Chiao et al., 2008; Chiao, Mathur, Harada, and Lipke, submitted for

\* Corresponding author at: Northwestern University, Department of Psychology, Cresap Hall, 2029 Sheridan Road, Evanston, IL 60208, United States.  
Tel.: +1 847 467 0481; fax: +1 847 491 7859.

E-mail address: [jchiao@northwestern.edu](mailto:jchiao@northwestern.edu) (J.Y. Chiao).

publication; Pineda, Sebestyen, & Naya, 1994) for recognizing social status signals from complex sensory input. A central question in the field of social neuroscience is to characterize how adaptive neurobiological mechanisms in human brain give rise to hierarchical social interaction. Despite rich understanding of how and when people communicate social status, very little is known about how the human brain enables social status inference.

Here we examine the nature of neural representations of social status hierarchy by comparing them to neural representations for knowledge in non-social domains such as number. The nature of mental and neural representations for knowledge of various conceptual domains is revealed by the cognitive mechanisms that operate on them. For example, people take longer to compare numbers that are closer in quantity (e.g., 64 vs. 65) relative to those farther in quantity (e.g., 10 vs. 65), a robust phenomenon known as the ‘numerical distance effect’ (Dehaene, Piazza, Pinel, & Cohen, 2003; Moyer & Landauer, 1967). The distance effect has also been demonstrated for other perceptual domains such as size (Moyer, 1973). Intriguingly, people also exhibit a ‘social status distance effect’ whereby people take a longer time to compare ranks that are close in social status (e.g., assistant versus associate professor), relative to ranks that are far in social status (e.g., janitor versus president of a university; Chiao, Bordeaux, & Ambady, 2004). Moreover, this status distance effect exists independent of the modality of the percept from which status is inferred. For example, Naval Reserve Officer Training Corp (NROTC) Midshipmen, who become experts in Navy social status hierarchy within the first year of their training, are able to compare social status from verbal (i.e., words like “Captain”) and nonverbal cues (i.e., visual uniform insignia) with equal ease and efficiency (Chiao et al., 2004). These results suggest that mental representations of social status hierarchy and number share a number of key properties in that knowledge in both domains is represented in a spatial, amodal and symbolic manner.

Given the similar characteristics between mental representations of numbers and social status, it is plausible that neural representations of knowledge of social status hierarchy and number are also shared. One possible candidate for a shared neural representation of knowledge of social status hierarchy and numbers is bilateral intraparietal sulci (IPS) which is widely regarded to play a special role in the internal representation of numerical magnitude both in human (Cohen-Kadosh et al., 2005; Dehaene et al., 2003; Pinel, Dehaene, Riviere, & LeBihan, 2001; Pinel, Piazza, Le Bihan, & Dehaene, 2004; Shuman & Kanwisher, 2004) and non-human primates (Neider, 2005; Sawamura, Shima, & Tanji, 2002) as well as comparing magnitude in other dimensions related to social status, such as size (Cohen-Kadosh et al., 2005; Pinel et al., 2004), time (Rao, Mayer, & Harrington, 2001), and space (Faillenot, Decety, & Jeannerod, 1999; Walsh, 2003). Recent meta-analyses of neuroimaging studies on numerical processing have found that the horizontal segment of the IPS (HIPS) is reliably engaged during multiple kinds of cognitive manipulations of numbers, as well as magnitude estimation of other magnitude dimensions such as physical size and luminance (Cohen-Kadosh, Lammertyn, & Izard, 2008; Dehaene et al., 2003). For instance, people demonstrate a physical size distance effect in reaction time and this behavioral distance effect corresponds to greater neural activation within the HIPS region for close relative to far size comparisons of numbers as well (Pinel et al., 2004). Additionally, greater activation within IPS is found during comparison of temporal, but not pitch, distance between two tones suggesting that the IPS is recruited not only during numerical processing but also temporal discrimination of auditory cues (Rao et al., 2001).

In the current study, we investigated the extent to which judgments about social status hierarchy and number engage distinct and overlapping neural regions of inferior parietal cortex. Specifi-

cally, we used fMRI to determine whether comparing social status of people, objects and symbols would recruit subregions of inferior parietal cortex, as has been previously shown with number comparisons. Given prior behavioral evidence of similarities in mental representations between social status and number, we hypothesized that subregions of inferior parietal cortex, which have been previously implicated in magnitude comparison of number, would also be recruited during social status comparisons.

## 1. Materials and methods

### 1.1. Participants

Twelve (6 females, age in years:  $M = 20.7$ ,  $SD = 1.23$ ) right-handed, college-aged Naval Reserve Officer Training Corp (NROTC) Midshipmen living in the Chicago, IL area participated in this study for payment. We controlled for participants’ level of social status hierarchy expertise by studying NROTC Midshipmen who had completed their first year of NROTC training, which includes learning of names, insignia, uniforms and appropriate salutes for various ranks in the US Navy, and use this knowledge in everyday social interaction with their peers, subordinates and superiors (Chiao et al., 2004). All participants in this study had normal or corrected-to-normal vision and gave informed written consent prior to participating in the experiment.

### 1.2. Stimuli

Stimuli consisted of 96 grey-scale photographs ( $560 \times 560$  pixels) of 24 Arabic numerals ranging from 33 to 99, 24 NROTC status insignias, 24 faces of NROTC officers and 24 2007 model Toyota cars (Fig. 1A). NROTC status insignias were used as stimuli because NROTC officers are experts at recognizing social status from these visual symbols. Faces of NROTC officers were also included in the current experiment in order to examine social status inferences made from more naturalistic stimuli. 2007 model Toyota cars were included to examine social status inference from familiar cultural objects. Accurate social status inference from cars, uniforms and faces used in the current experiment was not possible from obvious perceptual qualities of the stimuli (e.g., physical size of the car; number of stripes on a lapel) alone, without prior knowledge (i.e., learned associations of each stimulus and a given social status). Each of the four categories consisted of unique exemplars that were either close, medium or far in semantic distance from a predefined midpoint within each category. All photographs were matched for size, background color and luminosity in Adobe Photoshop™.

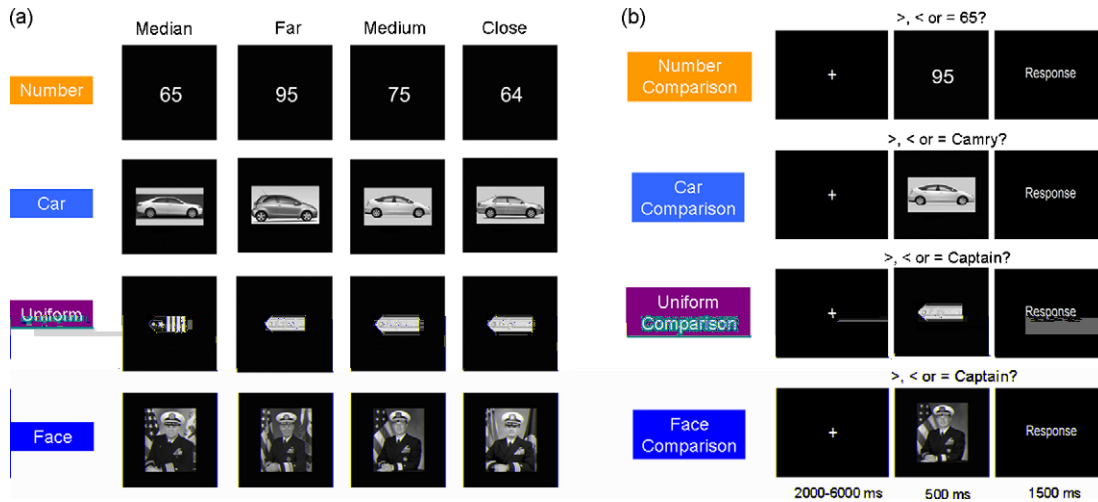
### 1.3. Procedure

We employed a block design of four functional runs. Each functional run included 3 blocks with 3 types of exemplars which varied in semantic distance (close, medium and far). Each block contained 8 trials of each exemplar type. Order of functional runs was counterbalanced across participants. For each functional run, participants viewed a grey-scale image of either a number, car, uniform or face for 500 ms followed by a 1500 ms screen prompting them to judge whether the stimulus presented was lower, equal or higher in magnitude (either in social status or number) to the categorical midpoint (Fig. 1B). Each of the four functional runs also included a control task, in which a subject pushed a button with their right index finger when the color of a cross hair presented at the center of the screen changed from white to red. We used the control task as a baseline to subtract neural responses due to motor processes.

For the number comparison run, participants judged whether a given number was less than, equal to or higher in magnitude relative to 65. For the status comparison of cars run, participants judged whether a given car was less than, equal to or higher in social status than a 2007 Toyota Camry. For status comparison of uniform insignia, participants judged whether a given uniform symbol or face was less than, equal to, or higher in social status relative to the uniform symbol for Naval Captain. For status comparison of NROTC officer faces, participants judged whether a facial photograph of a given officer was less than, equal to, or higher in social status relative to a Naval Captain, by inferring their social status from the officer’s uniform. Prior to entering the scanner, participants were given practice trials for each comparison task and shown visual examples of each midpoint in order to ensure familiarity with the comparison tasks.

### 1.4. Imaging parameters

Functional brain images were acquired at the Center for Advanced Medical Resonance Imaging (CAMRI) facility located in the Northwestern Medical Hospital in Chicago, IL. Scanning occurred on a 3.0 Tesla Siemens Trio MRI scanner equipped with single-shot, whole-body, echo planar image [repetition time (TR) = 2000 ms; echo time (TE) = 25 ms; flip angle = 70°; FOV = 20 cm,  $64 \times 64$  matrix; 34 slices; voxel size =  $3.0 \text{ mm} \times 3.0 \text{ mm} \times 4.0 \text{ mm}$ ], sensitive to BOLD contrast. A



**Fig. 1.** Examples of experimental materials. (a) Experimental stimuli used in the current experiment. (b) Sample trials of each type of comparison across all four domains.

high-resolution anatomical T1-weighted image was also acquired [TR=2300 ms; TE=2.91 ms; flip angle=9°; FOV=256 mm; 256 × 256 matrix; 176 slices; voxel size = 1.0 mm × 1.0 mm × 1.0 mm] for each subject. All stimuli were presented using Presentation software (Neurobehavioral Systems, Albany, CA) and projected onto a half-transparent viewing screen located behind the head coil. Subjects viewed the projected stimuli through a mirror.

### 1.5. Imaging processing and statistical analysis

Functional images were analyzed using SPM2 software (Wellcome Department of Imaging Neuroscience, London, UK) implemented in Matlab (Mathworks, Chesham, MA, USA). First, all volumes were realigned spatially to the first volume and a mean image was created. After a high-resolution image was coregistered onto the mean image, all volumes were normalized to the MNI (Montreal Neurological Institute) space using a transformation matrix obtained from the normalization process of the high-resolution image of each individual subject to the MNI template. The normalized images were then spatially smoothed with an 8 mm Gaussian kernel.

After preprocessing, statistical analysis for each individual subject was conducted using the general linear model (Friston et al., 1995). At the first level, each block of trials was modeled by convolving with a hemodynamic response function. For each subject, a linear regressor was applied to filter noise. In the subtraction analysis, 13 conditions [4 (domains: car, face, number, uniform) × 3 (distance: close, medium, far)] were modeled separately, including fixation. Random effects analyses were conducted by averaging the contrast images for each effect of interest. We visualized main effects (domain, distance) from random group analyses with Caret software (Van Essen et al., 2001) at  $p < 0.001$ , extent threshold = 10 voxels. Given the fact that we were investigating the neural correlates of small behavioral distance effects, we visualized random effect group interaction analyses (domain × distance) with Caret software (Van Essen et al., 2001) using a threshold of voxel-level  $p < 0.001$ , extent threshold = 5 voxels.

To further interrogate domain distance effects within different subregions of inferior parietal cortex, we functionally defined regions-of-interest within inferior parietal cortex as a sphere with a 16 mm diameter centered on a voxel with the peak value in the distance effect contrasts of close > far for each domain separately, at a statistical threshold previously used of  $p < 0.001$ , extent threshold = 10 voxels. Each domain distance effect (e.g., number) was used as an independent localizer run to isolate a subregion of inferior parietal cortex where the presence of a significant distance effect in other domains (e.g., uniform, car and face) could be investigated. MNI coordinates were converted to Talairach using a non-linear transformation (<http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>). Brodmann areas and brain regions were identified based on the Talairach Atlas (Talairach & Tournoux, 1988). Functional regions-of-interest analyses were performed using Marsbar software developed by Matthew Brett.

## 2. Results

### 2.1. Overall behavioral task performance

Consistent with prior research on mental representations of social status hierarchy and numbers (Chiao et al., 2004), we observed an overall significant main effect of semantic distance

on reaction time whereby people were slowest to compare closely related items ( $M=965$  ms,  $SE=48$ ) relative to far related items ( $M=847$  ms,  $SE=41$ ),  $F(2, 22)=12.25$ ,  $p < 0.0001$ . Within each of the four knowledge domains (number, face, uniform and car), a significant effect of semantic distance in reaction time was observed such that people were slower to compare items that were close, relative to those far, in meaning (Fig. 3). As previously shown, RT varied with numerical distance during number comparison [RT close – RT far = 105 ms;  $t(11)=3.50$ ,  $p < 0.01$ ]. Consistent to prior behavioral work (Chiao et al., 2004) for status comparison of uniforms, RT varied with status distance [RT close – RT far = 77 ms;  $t(11)=2.84$ ,  $p < 0.03$ ]. Moreover, during status comparison of faces, RT varied with status distance [RT close – RT far = 90 ms;  $t(11)=2.21$ ,  $p < 0.05$ ]. Additionally, during status comparison of cars, RT varied with status distance [RT close – RT far = 200 ms;  $t(11)=2.97$ ,  $p < 0.05$ ]. People were faster to compare numerical magnitude ( $M=699$  ms,  $SE=45$  ms) relative to magnitude of status in uniforms ( $M=908$  ms,  $SE=47$  ms),  $t(11)=5.50$ ,  $p < 0.0001$ , faces ( $M=1030$  ms,  $SE=48$ ),  $t(11)=7.59$ ,  $p < 0.0001$ , and cars ( $M=942$  ms,  $SE=55$  ms),  $t(11)=4.60$ ,  $p < 0.001$ . There was no significant interaction between domain and distance,  $F(6, 66)=0.89$ ,  $p > 0.5$ .

Across all four domains, overall accuracy was high ( $M=79.4$ ,  $SE=2.5$ ). People were more accurate at comparing numbers ( $M=91.4$ ,  $SE=1.6$ ) and social status of faces ( $M=84.0$ ,  $SE=3.73$ ), relative to uniforms ( $M=81.1$ ,  $SE=3.86$ ) and cars ( $M=61.1$ ,  $SE=4.80$ ),  $F(3, 33)=17.73$ ,  $p < 0.0001$ . Overall, there was also a significant main effect of distance on accuracy judgments,  $F(2, 22)=24.34$ ,  $p < 0.0001$ . During the number and face comparisons, accuracy did not significantly vary with semantic distance,  $p > 0.05$ . During status comparisons of uniforms and cars, accuracy did significantly vary with distance, [uniforms:  $t(11)=3.78$ ,  $p < 0.05$ ; cars:  $t(11)=6.76$ ,  $p < 0.01$ ]. People were more accurate for far [uniforms:  $M=85.0$ ,  $SE=0.04$ ; cars:  $M=74.5$ ,  $SE=0.06$ ] relative to close [uniforms:  $M=73.5$ ,  $SE=0.06$ ; cars:  $M=37.8$ ,  $SE=0.05$ ] comparisons for uniforms and cars. However, accuracy did not predict reaction time for responses across participants for either uniform comparisons,  $R^2=0.08$ ,  $p > 0.3$ , or car comparisons,  $R^2=0.22$ ,  $p > 0.1$ .

### 2.2. Bilateral intraparietal sulci is activated during social status and numerical comparison

In fMRI, magnitude comparisons of social status and number in all four domains elicited greater activation in bilateral IPS relative

**Table 1**  
Cerebral correlates of comparison tasks across domains, voxel-level  $p < 0.001$ , extant threshold = 10 voxels, cluster-level  $p < 0.05$  corrected.

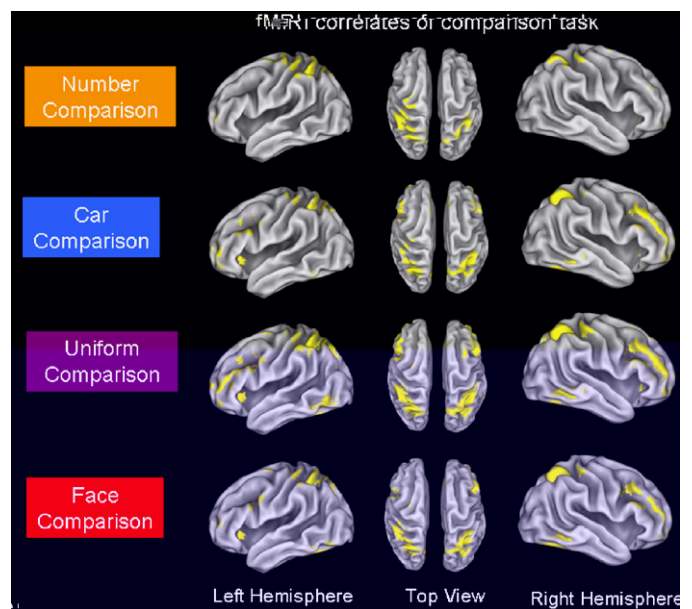
Task	X	Y	Z	Z score	BA	K	Brain area
Number comparison	-42	-45	66	5.28	5	575	L posterior superior parietal lobule
	-45	-36	51	4.92	40		L IPS
	-6	3	52	4.58	6	92	L medial frontal gyrus
	53	17	-3	4.58	47	75	R inferior frontal gyrus
	45	-44	55	3.79	40	78	R IPS
Uniform comparison	33	-62	42	12.93	19	808	R IPS
	56	-53	-6	7.69	37	528	R middle temporal gyrus
	-48	7	33	6.79	8	485	L middle frontal gyrus
	-3	14	52	6.44	6	340	L superior frontal gyrus
	-50	-35	49	6.41	40	765	L IPS
	36	23	-4	6.37	47	108	R inferior frontal gyrus
	-33	20	-1	6.3	47	91	L inferior frontal gyrus
	-30	-69	-44	5.93	19	80	L angular gyrus
	-42	-67	1	5.75	37	366	L inferior temporal gyrus
	50	14	38	5.63	8	836	R middle frontal gyrus
	33	2	50	5.44	6	63	R middle frontal gyrus
	0	-33	32	5.27	31	59	L cingulate gyrus
Face comparison	45	-42	-15	7.51	37	1442	R fusiform gyrus
	33	-62	42	7.1	19	485	R IPS
	-3	17	49	6.37	8	251	L superior frontal gyrus
	-30	-56	53	5.66	7	432	L IPS
	36	23	-4	5.64	47	65	R inferior frontal gyrus
	-36	20	-1	5.53	47	72	L inferior frontal gyrus
	53	24	24	5.32	46	448	R middle frontal gyrus
	3	-33	29	4.99	23	71	R cingulate gyrus
Car comparison	0	31	37	6.89	8	346	L medial frontal gyrus
	36	23	-7	6.42	47	81	R inferior frontal gyrus
	33	-62	42	6.06	19	358	R angular gyrus
	33	-59	53	5.55	7		R IPS
	-36	20	-1	5.78	47	83	L inferior frontal gyrus
	36	-39	-17	5.33	37	835	R fusiform gyrus
	-9	-77	-18	5.09	18	251	L cerebellum
	-36	-50	-14	4.38	37	130	L fusiform gyrus
	56	25	29	4.89	46	346	R middle frontal gyrus
	-30	-61	56	4.79	7	210	L posterior superior parietal lobe
	-45	52	0	4.27	47	78	L inferior frontal gyrus
	-33	-50	47	4.06	40	58	L IPS

to the baseline condition (Table 1 and Fig. 2). As previously shown (Dehaene et al., 2003), number comparisons also elicited activation in the left posterior superior parietal lobe and right inferior frontal gyrus. Similar to numerical comparisons, status comparisons of uniforms, faces and cars also activated bilateral inferior frontal gyrus. Hence, as predicted, both social status and numerical comparisons elicited greater activation in neural regions previously implicated in magnitude processing including bilateral IPS and inferior frontal gyrus.

Direct contrasts of whole-brain activation across different comparison domains yielded no differential activation within the bilateral intraparietal sulci region (all  $p$ 's  $> 0.001$ ). Greater activation in the right middle frontal gyrus was observed for uniform status comparisons relative to car status comparisons ( $p < 0.001$ ). No other brain regions demonstrated greater activation across domain comparisons ( $p > 0.001$ ).

**2.3. Distinct and overlapping neural representations of social status hierarchy and number located within subregions of human inferior parietal cortex**

To more precisely characterize the nature of neural representations underlying knowledge of social status hierarchy and number, we examined whether a neural distance effect parallel to that seen in behavior was observable within subregions of human inferior parietal cortex. Replicating previous neuroimaging studies of numerical processing (Dehaene et al., 2003) whole-brain analyses



**Fig. 2.** fMRI correlates of comparison task across all domains. Activation maps are shown at a threshold of voxel level  $p < 0.001$ , cluster level,  $p < 0.05$  corrected for multiple comparisons.



Table 2  
Cerebral correlates of distance effects across domains, voxel-level  $p < 0.001$ , extant threshold = 10 voxels.

Task	X	Y	Z	Z score	BA	K	Brain area
Number distance	Š36	Š53	52	4.47	7	129	L superior parietal lobule
	Š54	Š41	49	3.27	21		L IPS
	50	Š38	46	4.32	32	108	R IPS
	33	59	16	4.01	22	21	R middle frontal gyrus
	6	Š73	45	3.89	47	74	R precuneus
	65	Š18	Š4	3.84	40	27	R middle temporal gyrus
	0	22	38	3.73	31	31	L anterior cingulate gyrus
	42	17	Š8	3.47	40	11	R inferior frontal gyrus
Uniform distance	3	11	55	4.58	40	49	R superior frontal gyrus
	53	Š45	35	4.56	7	103	R IPS
	59	Š37	10	4.4	21	43	R superior temporal gyrus
Face distance	53	Š48	33	4.02	7	35	R IPS
	9	Š47	55	3.73	40	12	R precuneus
	53	Š24	Š6	3.65	7	14	R middle temporal gyrus
	Š48	Š32	4	3.45	37	15	L superior temporal gyrus
Car distance	Š27	Š68	37	4.07		240	L precuneus
	Š45	Š35	49	3.95	7		L IPS
	Š33	Š56	50	3.85	22		L posterior superior parietal lobule
	Š45	Š70	1	3.9	6	19	L inferior temporal gyrus
	Š27	0	58	3.79		19	L middle frontal gyrus
	Š9	Š20	12	3.73	9	15	L thalamus
	48	Š52	11	3.55		11	R superior temporal gyrus
	9	Š11	9	3.43		10	R thalamus
Š42	25	32	3.38		10	L middle frontal gyrus	

revealed a numerical distance effect within several regions of parietal and frontal cortex, including the bilateral horizontal segment of IPS, bilateral precuneus, right superior and inferior frontal gyrus and anterior cingulate gyrus ( Table 2).

Supporting our hypotheses of shared neural representations underlying social status hierarchy and number, whole-brain analyses also revealed greater activity within left IPS for close relative to far social status comparisons of cars and within right IPS for

Fig. 3. Behavioral and neural correlates of the distance effect across all domains. Activation maps are thresholded at voxel level  $p < 0.001$ , extant threshold = 10 voxels. Green circles indicate anatomically defined regions of left and right intraparietal sulcus. Blue circles indicate left ( X = Š44, Y = Š48, Z = 47) and right ( X = Š41, Y = Š47, Z = 48) horizontal segment of IPS as defined by the Dehaene et al. (2003) meta-analysis. Red circles indicate anatomically defined regions of left and right angular gyrus.

**Table 3**  
Cerebral correlates of distance × domain interaction, voxel-level  $p < 0.001$ , extant threshold = 5 voxels.

Task	X	Y	Z	Z-score	BA	K	Brain area
Number[C-F] – Uniform[C-F]	No suprathreshold clusters						
Number[C-F] – Face[C-F]	-27	-59	47	3.57	7	11	L IPS
	-48	11	35	3.35	9	6	L middle frontal gyrus
	45	7	33	3.21	9	5	R middle frontal gyrus
Number[C-F] – Car[C-F]	No suprathreshold clusters						
Uniform[C-F] – Number[C-F]	-9	52	-8	4.15	10	18	L superior frontal gyrus
	9	59	8	3.97	10	14	R superior frontal gyrus
	-3	40	-20	3.82	11	33	L orbitofrontal gyrus
Uniform[C-F] – Face[C-F]	No suprathreshold clusters						
Uniform[C-F] – Car[C-F]	No suprathreshold clusters						
Face[C-F] – Number[C-F]	-48	-35	5	4.72	21	27	L superior temporal sulcus
	50	-51	36	3.87	40	17	R IPS
	-12	49	-10	3.84	32	61	L anterior cingulate gyrus
	21	-74	26	3.74	19	13	R orbital gyrus
	-18	-35	-8	3.60		8	L hippocampal gyrus
	-18	50	17	3.48	10	7	L superior frontal gyrus
	12	52	0	3.37	32	9	R anterior cingulate gyrus
Face[C-F] – Uniform[C-F]	No suprathreshold clusters						
Face[C-F] – Car[C-F]	0	35	-7	3.94	24	17	Cingulate gyrus
	50	-56	36	3.76	40	9	R IPS
Car[C-F] – Number[C-F]	-45	18	16	4.27	45	12	L inferior frontal gyrus
	48	-52	11	3.39	21	8	R superior temporal sulcus
Car[C-F] – Uniform[C-F]	-27	9	55	4.08	6	5	L middle frontal gyrus
	-18	-62	42	3.51	7	6	L IPS
Car[C-F] – Face[C-F]	-27	-68	34	3.81	39	23	L angular gyrus
	-24	-67	50	3.56	7	8	L IPS
	36	-56	50	3.53	40	11	R inferior parietal lobe
	45	-56	-10	3.41	37	13	R fusiform gyrus
	24	2	-13	3.41		5	R amygdala

close relative to far social status comparisons of faces and uniforms (Table 2 and Fig. 3; all  $p$ 's < 0.001). Additional brain regions within frontal, parietal and temporal cortices also demonstrated greater activation for close relative to far comparisons across different domains (Table 2). For the numerical comparison task, greater activation was found in bilateral precuneus, right supramarginal gyrus, right middle and superior temporal gyrus, right inferior, middle and superior frontal gyrus and left cingulate gyrus. For the uniform status comparison task, greater activation was observed in right superior and inferior frontal gyrus as well as right middle and superior temporal gyrus. For the face status comparison task, an increased response for close relative to far comparisons was found in bilateral precuneus, right middle temporal gyrus, left superior temporal gyrus and left cingulate gyrus. For the car status comparison task, neural status distance effects were found for left precuneus, bilateral posterior superior parietal lobule, bilateral middle frontal gyrus, bilateral thalamus, left inferior temporal gyrus and right superior temporal gyrus.

Additionally, we conducted whole-brain voxel-wise analyses to identify subregions of inferior parietal cortex that demonstrated a significant domain × distance interaction (Table 3). Greater left IPS activation was found for numerical relative to face distance effects as well as car relative to uniform and face distance effect whereas greater right IPS was observed for face relative to number and uniform distance effects ( $p < 0.001$ ).

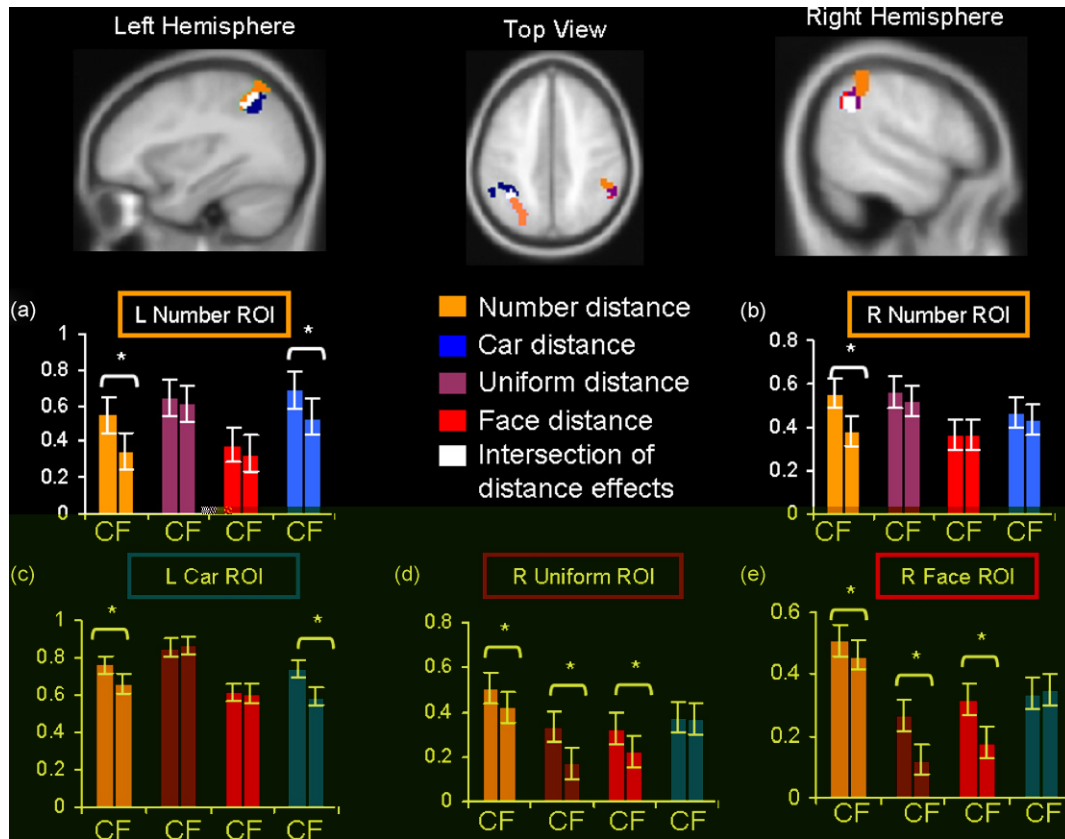
To further interrogate the location, magnitude and overlap of social status and numerical distance effects, we conducted a functionally defined ROI analysis across the four domains within five subregions of bilateral human inferior parietal cortex (Table 4). Percent signal change analyses within these five subregions of IPS revealed a significant ROI location × domain × distance interaction,

$F(12, 132) = 12.27, p < 0.0001$ . In the number-defined ROI located within the left IPS (peak coordinate:  $X = -54, Y = -41, Z = 49$ ), there was a significant distance (close, far) × domain (car, face, uniform) interaction,  $F(2, 22) = 3.52, p < 0.05$ . A significant car distance effect was also observed in 10 out of 12 participants [% signal change close – % signal change far = 0.15;  $t(11) = 4.30, p < 0.001$ ] (Fig. 4a). In the number-defined ROI located within the right IPS (peak coordinate:  $X = 50, Y = -38, Z = 46$ ), no significant distance effects in any other domain was observed (all  $p$ 's > 0.1; Fig. 4b).

In the car-defined ROI located within the left IPS (peak coordinate:  $X = -45, Y = -35, Z = 49$ ), there was a significant distance (close, far) × domain (face, number, uniform) interaction,  $F(2, 22) = 5.61, p < 0.01$ . A significant number distance effect was also observed in 10 out of 12 participants [% signal change close – % signal change far = 0.10;  $t(11) = 5.03, p < 0.0004$ ] (Fig. 4c). In the uniform-defined ROI located within right IPS (peak coordinate:  $X = 53, Y = -45, Z = 35$ ), there was a significant distance (close, far) × domain (car, face, number) interaction,  $F(2, 22) = 4.73, p < 0.02$ . A significant distance effect was also observed in the number domain for 12 out of 12 participants [% signal change close – % signal change far = 0.19;

**Table 4**  
Cerebral correlates of intersection of distance effects across domains, voxel-level  $p < 0.001$ , extant threshold = 10 voxels.

Task	X	Y	Z	Z-score	BA	K	Brain area
Intersection	-3	14	49	4.28	6	51	L superior frontal gyrus
	-48	-35	52	4.01	40	34	L IPS
	-36	20	2	3.98	13	10	L insula
	-36	-53	55	3.97	7	56	L superior parietal lobe
	45	-47	55	3.64	40	36	R IPS
	42	20	-4	3.61	47	13	R inferior frontal gyrus



**Fig. 4.** Functional region-of-interest analyses within subregions of human inferior parietal cortex. Colored ROIs illustrate location of the cluster including the voxel with the peak value for each of the distance effects (C=close semantic distance; F=far semantic distance) across domains. White voxels indicate neuroanatomical location of intersection of neural distance effects within IPS across domains (left IPS:  $X=-48, Y=-35, Z=52$ ; right IPS:  $X=45, Y=-47, Z=55$ ) (Table 4). Neural distance effects were observed within (a–b) left and right IPS for number (orange), (c) left IPS for cars (blue) and within right IPS for (d–e) number, uniform (purple) and face (red) domains.

$t(11)=5.19, p<0.0003$ ] and in the face domain for 10 out of 12 participants [% signal change close – % signal change far=0.11;  $t(11)=4.28, p<0.001$ ] (Fig. 4d). Additionally, in the face-defined ROI located within right IPS (peak coordinate:  $X=53, Y=-48, Z=33$ ), there was a significant distance (close, far)  $\times$  domain (car, number, uniform) interaction,  $F(2, 22)=6.29, p<0.007$ . A significant distance effect was also observed in the number domain in 11 out of 12 participants [% signal change close – % signal change far=0.05;  $t(11)=4.32, p<0.001$ ] and in the uniform domain in 11 out of 12 participants [% signal change close – % signal change far=0.14;  $t(11)=4.91, p<0.0004$ ] (Fig. 4e).

### 3. Discussion

Both social status hierarchy and numerical comparisons recruited distinct and overlapping regions of inferior parietal cortex. In particular, bilateral intraparietal sulci were recruited during the process of numerical and social status magnitude. Additionally, bilateral intraparietal sulci displayed a neural distance effect, whereby neural activity increased for close relative to far comparisons. Specifically, neural distance effects for number and social status of cars were observed within left IPS and neural distance effects for number and social status of faces and uniforms were observed within right IPS, suggesting overlapping neural representations of knowledge of car status hierarchy and number. Taken together, these results suggest two roles for subregions of inferior parietal cortex in social status and numerical processing: (1) comparing exemplars within each continuum (a ‘process’ effect) and (2) representing knowledge of numbers as well as knowl-

edge of social status hierarchy of people and objects (a ‘content’ effect).

These findings are remarkable given previous demonstrations of response selectivity in subregions of human inferior parietal cortex, such as IPS, across different comparison tasks (Dehaene et al., 2003; Pinel et al., 2004) and, in particular, the absence of IPS recruitment during semantic judgments which have also been shown to produce a behavioral distance effect. For instance, a previous behavioral study reported a behavioral semantic distance effect for animal trait comparisons such that people were slower to judge the ferocity or intelligence of closely related animals (e.g., tiger vs. lion) relative to far-related animals (e.g., mouse vs. elephant; Banks & Flora, 1977). However, a subsequent PET study showed that this behavioral distance effect was associated with greater activation in inferior temporal gyrus, rather than bilateral IPS, suggesting that not all kinds of magnitude comparisons necessarily recruit bilateral intraparietal regions (Thioux, Pesenti, Costes, De Volder, & Seron, 2005). Hence, results from this study provide novel evidence of neural representations of magnitude in inferior parietal cortex that are not only for perceptual and cognitive domains including number and space, but also for domains of social knowledge such as social status hierarchy.

In the current study, a broad network of brain regions was recruited during social status comparisons. Consistent with prior social neuroscience research, social status comparisons engaged a network of brain regions within occipitotemporal and frontal cortices that are typically recruited during social cognition. Greater activation in bilateral fusiform gyrus was found for social status comparisons of uniforms, faces and cars, a region previously shown

to respond preferentially to faces (Kanwisher, McDermott, & Chun, 1997) but also increase in response to familiar symbols (Baker et al., 2007) and objects (Haxby et al., 2001). Social status comparisons of people, symbols and objects also robustly activated the posterior portion of rostral medial prefrontal gyrus (prMFC), a result consistent with previous studies showing recruitment of this region during decision-making and action selection (Amodio & Frith, 2006). Increased prMFC activity during social status comparison may reflect greater engagement of neural processes during identification of and response selection to high and low social status individuals, symbols and objects.

In addition, we observed a lateralization in neural distance effects in inferior parietal cortex associated with social status comparison. Left intraparietal sulcus activation was found for status comparisons of cars while right IPS activation was found for status comparisons of NROTC uniforms and faces of NROTC officers. A rich body of neuroimaging and neuropsychological studies indicates a relative advantage of the right hemisphere for global (i.e., perceiving to the whole stimulus) relative to local (i.e., perceiving to focal aspects of the stimulus) processing (Hutsler & Galuske, 2003). For instance, previous neuropsychology and neuroimaging work has shown that only right-lateralized parietal regions are engaged during numerical estimation relative to numerical counting (Piazza, Mechelli, Price, & Butterworth, 2006). A robust right-lateralized advantage has also been observed in cortical and subcortical regions (e.g., superior temporal gyrus, fusiform, amygdala) associated with a number of social cognitive and emotional tasks (e.g., inferring eye gaze direction, facial identity or fear recognition; Noesselt, Driver, Heinze, & Dolan, 2005; Pelphrey, Viola, & McCarthy, 2004). We speculate that greater engagement of right IPS during social status comparison of NROTC uniforms and faces may indicate the use of a global strategy to estimate social status from uniforms or faces, but use of a finer-grained local strategy to infer the relative social status of cars. Differences in hemispheric engagement within IPS during social status comparison may also be due to differences in the category of stimuli being compared; comparison of NROTC uniforms and faces involves evaluating the social status of people, whereas social status comparison of cars involves evaluating the social status of objects.

Why are neural representations of social status hierarchy and number within human inferior parietal cortex both distinct and overlapping? One hypothesis is that individual neurons within the inferior parietal region code for magnitude of different continuous dimensions (Pinel et al., 2004; Walsh, 2003). According to this view, individual neurons within inferior parietal cortex encode stimuli along a single dimension (e.g., number, space, social status), however, the spatial distribution of these neurons within IPS is functionally heterogeneous such that no localized patch of IPS neurons only code stimuli along a single dimension (Pinel et al., 2004). Hence, each type of magnitude comparison recruits functionally distinct but spatially overlapping neurons and thus, neural representations of number and social status hierarchy appear to be both distinct and overlapping. This distributed and overlapping coding theory explains why activation associated with social status and numerical comparison and distance effects would partially overlap even though highly specialized individual neurons dedicated to magnitude estimation code for only one continuous dimension, such as 'numerons', single neurons within monkey parietal cortex specialized for numerical processing (Neider, Diester, & Tuduscius, 2006; Neider, Freedman, & Miller, 2002; Sawamura et al., 2002; Walsh, 2003) and even possibly, single neurons or neuronal populations specialized for social status inferences. Future research in single-cell recording in awake monkeys may be able to determine whether specialized cells within inferior parietal cortex that are selective to social status magnitude exist or not.

Another plausible explanation for overlapping neural representations of social status hierarchy and number is that social status inference requires simultaneous multidimensional comparisons of numerical, spatial and temporal magnitude. As discussed earlier, differentiating people of high social status and low social status often involves perceiving differences in spatial and temporal qualities of social signals communicated during a social interaction. Rather than recruiting specialized neurons for social status inference, social status comparison may simultaneously require convergent computation of magnitude across multiple dimensions which are represented within inferior parietal cortex. A recent study demonstrated the topography of five distinct visual maps within IPS supporting the notion of functional subdivision within the medial bank of IPS, and more specifically, the possibility of magnitude representations across multiple continua within or across these subregions (Swisher, Halko, Merabet, McMains, & Somers, 2007). One way to test this hypothesis is by using neuropsychological methods to examine social status inference in patients with focal parietal lesions and impaired spatiotemporal and/or numerical comparison abilities. If successful detection of social status signals is necessarily contingent upon the ability to infer magnitude along more primitive continuous dimensions (i.e., number, space and time), then an inability to infer magnitude in one or more of these dimensions should result in a subsequent impairment of accurate social status inference. Intact competence in social status inference but not magnitude estimation in other cognitive or perceptual domains would suggest a dissociation in neural mechanisms underlying the knowledge of social status hierarchy and number.

A third plausible explanation is that both social status and numerical comparisons recruit IPS because they involve some aspect of ordinal knowledge representation. For instance, a recent prior neuroimaging study found that HIPS was equally responsive to comparisons of number and letters, both symbolic systems involving ordinal knowledge representation (Fias, Lammertyn, Caessens, & Orban, 2007) suggesting that ordinality, in addition to numerosity, is coded within this region. By extension to the current experiment, it is plausible that the overlapping neural distance effects observed within inferior parietal cortex reflect the ordinal component inherent in both social status (e.g., Commander is followed by Captain) and number (e.g., 47 is followed by 48) knowledge domains. However, this does not necessarily rule out the possibility that distinct neuronal populations with IPS encode both cardinality and ordinality, though the current experiment cannot address this alternative account given the limited spatial and temporal resolution of fMRI. Additionally, there are other examples of knowledge domains that similarly contain an ordinal component, such as the ferocity of animals (Thioux et al., 2005) as well as the intelligence and height of other people (Lindner, Hundhammer, Ciaramidaro, Linden, & Mussweiler, 2008), but do not appear to recruit neuronal populations within IPS during comparison judgments. Hence, we suggest that neural distance effects associated with social status comparisons observed in the current study may not necessarily be due to the ordinal nature of social status knowledge.

A fourth explanation for the current findings is that both social status and numerical comparison tasks involve tasks of considerable difficulty and activation within inferior parietal cortex reflects, at least in part, heightened task demand during both kinds of comparisons, rather than evidence of internal representations of knowledge per se (Gobel, Johansen-Berg, Behrens, & Rushworth, 2004). Several prior studies have reported greater activation within subregions of inferior parietal cortex for a variety of unrelated difficult and attention-demanding tasks (Shuman & Kanwisher, 2004). However, results from this study suggest that it is unlikely that the



greater inferior parietal cortex activation for social status and number comparison is due solely to task difficulty. Behavioral results from the current study indicate that people found car status comparisons relatively more difficult than numerical comparisons and status comparisons from uniforms and faces. Yet, the magnitude of the neural distance effect within left IPS was greater for numerical comparison relative to car social status comparison and no neural distance effect within right IPS was found for car status comparisons. Moreover, several other studies specifically examining the influence of task difficulty on behavioral and neural distance effects have still found greater IPS activation during numerical processing (Ansari, Fugelsang, Dhital, & Venkatraman, 2006; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003). Hence, findings from the present study and prior studies indicate that greater activation within subregions of left and right inferior parietal cortex for close relative to far comparisons of numerical and social status magnitude is not likely due to task difficulty alone, but instead is a genuine reflection of internal representations for knowledge of numbers and social status hierarchy.

In summary, here we show that subregions of inferior parietal cortex are activated during the comparison of numerical and social status magnitude. Moreover, degree of activation within bilateral intraparietal sulci corresponds with semantic distance in both social status and number domains. Despite a rich understanding of how the human brain performs perceptual and cognitive comparisons, very little is known about how the brain makes social status comparisons and represents knowledge of social status. Findings from the present study provide a foundation for future investigations into the role of inferior parietal cortex in neural representations of social status hierarchy and possibly other social dimensions, more broadly construed.

## Acknowledgments

The authors thank Melinda Chan and Xiaoxi Liu for help with stimuli preparation, Donald Redding and Captain James Otis, from the Northwestern Naval ROTC Unit, for invaluable assistance with participant recruitment, and Paul Reber, Mark Jung-Beeman, Jennifer Richeson and Steven Franconeri for helpful discussion. This work is supported by NSF BCS-0720312 and NSF BCS-0722326 to J.Y.C.

## References

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, 4, 267–278.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, 7, 268–277.
- Ansari, D., Fugelsang, J. A., Dhital, B., & Venkatraman, V. (2006). Dissociating response conflict from numerical magnitude processing in the brain: an event-related fMRI study. *Neuroimage*, 32, 799–805.
- Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experimental origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences*, 104, 9087–9092.
- Banks, W. P., & Flora, J. (1977). Semantic and perceptual processes in symbolic comparisons. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 278–290.
- Boehm, C. (1999). *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Cambridge: Harvard University Press.
- Cheney, S. L., & Seyfarth, R. M. (1990). The representation of social relations by monkeys. *Cognition*, 37, 167–196.
- Chiao, J. Y., Bordeaux, A. R., & Ambady, N. (2004). Mental representations of social status. *Cognition*, 93, B49–B57.
- Chiao, J. Y., Adams, R. B., Jr., Tse, P. U., Lowenthal, W. T., Richeson, J. A., & Ambady, N. (2008). Knowing who's boss: fMRI and ERP investigations of social dominance perception. *Group Relations and Intergroup Processes*, 11(2), 201–214 (Special Issue in Social Neuroscience)
- Chiao, J.Y., Mathur, V.A., Harada, T., Lipke, T. (submitted for publication). Preference for human social hierarchy as a function of empathic neural response.
- Cohen-Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., Van de Ven, V., Zorzi, M., Hendler, T., Goebel, R., & Linden, D. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, 43, 1238–1248.
- Cohen-Kadosh, R., Lammertyn, J., & Izard, V. (2008). Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Progress in Neurobiology*, 84, 132–147.
- Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., & Tsivkin, S. (1999). Sources of mathematical thinking: Behavioral and brain imaging evidence. *Science*, 284, 970–974.
- Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, 20, 487–506.
- Dovidio, J. F., & Ellyson, S. L. (1982). Decoding visual dominance: Attributions of power based on relative percentages of looking while speaking and looking while listening. *Social Psychology Quarterly*, 45, 106–113.
- Ellyson, S. L., & Dovidio, J. F. (1985). *Power, dominance, and nonverbal behavior*. New York: Springer-Verlag.
- Eger, E., Sterzer, P., Russ, M. O., Giraud, A.-L., & Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, 37, 719–725.
- Erk, S., Spitzer, M., Wunderlich, A. P., Galley, L., & Walter, H. (2002). Cultural objects modulate reward circuitry. *Neuroreport*, 13, 2499–2503.
- Faillenot, I., Decety, J., & Jeannerod, M. (1999). Human brain activity related to the perception of spatial features of objects. *Neuroimage*, 10, 114–124.
- Fias, W., Lammertyn, J., Caessens, B., & Orban, G. A. (2007). Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. *Journal of Neuroscience*, 27(33), 8952–8956.
- Fiske, A. P. (1992). The four elementary forms of sociality: Framework for a unified theory of social relations. *Psychological Review*, 99, 689–723.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., Frith, C., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- Gobel, S. M., Johansen-Berg, H., Behrens, T., & Rushworth, M. F. S. (2004). Response-selection-related parietal activation during number comparison. *Journal of Cognitive Neuroscience*, 16, 1536–1551.
- Grosenick, L., Celement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature*, 445, 429–432.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293, 2425–2430.
- Hutsler, J., & Galuske, R. A. W. (2003). Hemispheric asymmetries in cerebral cortical networks. *Trends in Neuroscience*, 26, 429–435.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: An extrastriate region specialized for face perception. *Journal of Neuroscience*, 17, 4302–4311.
- Lindner, M., Hundhammer, T., Ciaramidaro, A., Linden, D. E., & Mussweiler, T. (2008). The neural substrates of person comparison: an fMRI study. *Neuroimage*, 40(2), 963–971.
- Maestripieri, D. (1996). Primate cognition and the bared-teeth display: A reevaluation of the concept of formal dominance. *Journal of Comparative Psychology*, 110, 402–405.
- Moyer, R. S., & Landauer, T. K. (1967). Time required for judgments of numerical inequality. *Nature*, 215, 1519–1520.
- Moyer, R. S. (1973). Comparing objects in memory—evidence suggesting an internal psychophysics. *Perception and Psychophysics*, 13, 180–184.
- Neider, A. (2005). Counting on neurons: the neurobiology of numerical competence. *Nature Reviews Neuroscience*, 6, 177–190.
- Neider, A., Diester, I., & Tuduscius, O. (2006). Temporal and spatial enumeration processes in the primate prefrontal cortex. *Science*, 313, 1431–1435.
- Neider, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science*, 297, 1708–1711.
- Noesselt, T., Driver, J., Heinze, H.-J., & Dolan, R. (2005). Asymmetrical activation in the human brain during processing of fearful faces. *Current Biology*, 15, 424–429.
- Pelphrey, K. A., Viola, R. J., & McCarthy, G. (2004). When strangers pass: processing of mutual and averted social gaze in the superior temporal sulcus. *Psychological Science*, 15, 598–603.
- Piazza, M., Mechelli, A., Price, C. J., & Butterworth, B. (2006). Exact and approximate judgments of visual and auditory numerosity: An fMRI study. *Brain Research*, 1106, 177–188.
- Pineda, J. A., Sebestyen, G., & Naya, C. (1994). Face recognition as a function of social attention in non-human primates: an ERP study. *Brain Research Cognition. Brain Research*, 2, 1–12.
- Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *Neuroimage*, 14, 1013–1026.
- Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, 41, 983–993.
- Pinker, S. (1997). *How the Mind Works*. New York: W.W. Norton & Company.
- Rao, S. M., Mayer, A. R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience*, 4, 317–323.
- Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. *Nature*, 415, 918–921.

- Schjelderup-Jebbe, T. (1935). Social behavior of birds. In C. Murchison (Ed.), *A Handbook of Social Psychology* (pp. 947–972). Worcester: MA.
- Shuman, M., & Kanwisher, N. (2004). Numerical magnitude in the human parietal lobe: Tests of representational generality and domain specificity. *Neuron*, *44*, 1–20.
- Sidanius, J., & Pratto, F. (2001). *Social dominance orientation: A theory of intergroup of hierarchy and oppression*. New York: Cambridge University Press.
- Swisher, J. D., Halko, M. A., Merabet, L. B., McMains, S. A., & Somers, D. C. (2007). Visual topography of human intraparietal sulcus. *Journal of Neuroscience*, *27*, 5326–5337.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system—an approach to cerebral imaging*. New York: Thieme Medical Publishers.
- Thioux, M., Pesenti, M., Costes, N., De Volder, A., & Seron, X. (2005). Task independent semantic activation for numbers and animals. *Cognitive Brain Research*, *24*, 284–290.