

# Supplemental Information

## *The Distributed Nature of Working Memory*

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	Species	N	Stimuli	Task		Signal	Brain Areas	Specificity	N of Contents		Notes
				Type	Precision				Trial	Analysis	
[1] Buschmann et al., 2011	rhesus monkey	2	color arrays	change detection	identity	neural spiking	IPFC; IIPC; FEF	color	2-5	6; 14	2 colors per location per session
[2] Fuster & Jervey, 1981	rhesus monkey	9	colored compl. shapes	DMTS	identity	neural spiking	IT	color	1	2-4	
[3] Fuster & Jervey, 1982	rhesus monkey	7	colored lights	DMTS	identity	neural spiking	IT	color	1	2-4	
[4] Fuster, 1990	rhesus monkey	4	colored compl. shapes	DMTS	identity	neural spiking	IT	color & shape identity	1	2	symbolic cues for encoding
[5] Xing et al., 2013	human	5	moving gratings	change discrimination	contrast: $\pm 20\%$	BOLD	VC: V1-V3	contrast	1	2	retro-cue; ROIs
[6] Riggall & Postle, 2012	human	10	motion flow fields	change detection	titrated to threshold	BOLD	VC	direction	1	4	retro-cue; ROIs
[7] Emrich et al., 2013	human	10	motion flow fields	delayed estimation	detailed recall	BOLD	hMT+; VC: V1-V2, IOS	direction	1-3	3	ROIs
[8] Swaminathan et al., 2013	rhesus monkey	2	motion flow fields	DMTC	categorical	neural spiking	PPC: LIP, MIP	direction category	1	2 (3)	
[9] Rishel et al., 2013	rhesus monkey	2	motion flow fields	DMTC	categorical	neural spiking	PPC: LIP	direction category	1	2 (2)	resistant to saccadic suppression
[10] Bisley et al., 2004	rhesus monkey	2	motion flow fields	change detection	direction $\pm 180^\circ$	neural spiking	MT	direction	1	4	
[11] Zaksas & Pasternak, 2006	rhesus monkey	2/2	motion flow fields	change detection	titrated to threshold	neural spiking	MT; IPFC	direction	1	4	IMC
[12] Mendoza-Halliday et al., 2014	rhesus monkey	2	motion flow fields	change detection	$\pm 90^\circ$ ra	<sup>(a)</sup> neural spiking <sup>(b)</sup> local field potentials	(a) MST; IPFC (b) MT	direction	1	4	MT null-effect for spiking
[13] Hussar & Pasternak, 2012	rhesus monkey	2	motion flow fields	change detection	direct.: $\pm 10-90^\circ$ ra speed: x0.1-x3	neural spiking	IPFC	direction	1	2	IMC
[14] Wimmer et al., 2016	rhesus monkey	2	motion flow fields	change detection	direct.: $\pm 10-90^\circ$ ra speed: x0.1-x3	local field potentials	IPFC	direction, speed	1	2	
[15] Sarma et al., 2016	rhesus monkey	4	motion flow fields	DMTS; DMTC	$45^\circ-75^\circ$ ra; categorical	neural spiking	IPFC; PPC: LIP	direction; dir. category	1	8; 2 (4)	direction null-effect in PPC
[16] Lemus et al., 2009	rhesus monkey	2	auditory flutter	change discrimination	$\pm 12$ Hz	neural spiking	PM: VPM	frequency	1	7	parametric effect
[17] Vergara et al., 2016	rhesus monkey	2	tactile & auditory flutter	change discrimination	$\pm 8$ Hz	neural spiking	PM: MPM	frequency	1	7	parametric effect;
[18] Spitzer et al., 2010	human	14	tactile flutter	change discrimination	$\pm 5$ Hz	EEG $\alpha/\beta$ power	IPFC ( $\beta$ );	frequency	1	4	parametric effect; source localization
[19] Spitzer & Blankenburg, 2011	human	25	tactile flutter	change discrimination	$\pm 4$ Hz	EEG $\beta$ power	IPFC ( $\beta$ )	frequency	1	8	parametric effect; source localization; retro-cue
[20] Romo et al., 1999	rhesus monkey	4	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	IPFC	frequency	1	7	parametric effect
[21] Brody et al., 2003	rhesus monkey	5	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	IPFC	frequency	1	7	parametric effect;

[22] Barak et al., 2010	rhesus monkey	2	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	IPFC	frequency	1	7	parametric effect;
[23] Hernández et al., 2002	rhesus monkey	4	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	PM: MPM	frequency	1	11	parametric effect
[24] Hernández et al., 2010	rhesus monkey	4	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	PM: M/D/V; IPFC; SC: S2	frequency	1	11	parametric effect
[25] Romo et al., 2002	rhesus monkey	4	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	S2	frequency	1	8	parametric effect
[26] Salinas et al., 2000	rhesus monkey	3	tactile flutter	change discrimination	$\pm 8$ Hz	neural spiking	S2	frequency	1	7	parametric effect
[27] Spitzer & Blankenburg, 2012	human	28	vis. flicker, tac. & aud. flutter	change discrimination	$\pm 4$ Hz	EEG $\beta$ power	IPFC ( $\beta$ )	frequency	1	8	parametric effect; source localization
[28] Chelazzi et al., 2001	rhesus monkey	2	natural images	DMTS	identity	neural spiking	V4	image identity	1	24	
[29] Miller et al., 1993	rhesus monkey	2	natural images	DMTS	identity	neural spiking	IT	image identity	1	6	nonmatching items as distractors
[30] Chelazzi et al., 1998	rhesus monkey	3	natural images	DMTS	identity	neural spiking	IT	image identity	1	24	
[31] Chelazzi et al., 1993	rhesus monkey	3	natural images	DMTS	identity	neural spiking	IT	image identity	1	24	
[32] Miller et al., 1996	rhesus monkey	2	natural images	DMTS	Identity	neural spiking	IPFC	image identity	1	6	nonmatching items as distractors
[33] Asaad et al., 2000	rhesus monkey	2	natural images	DMTS	identity	neural spiking	IPFC	image identity	1	2	includes response-correlated spatial tasks
[34] Hayden & Gallant, 2013	rhesus monkey	2	natural images	DMTS	identity	neural spiking	V4	image identity; location	1	2; 2	nonmatching items as distractors
[35] Rainer et al., 1998	rhesus monkey	2	natural images & location	DMTS	identity; 5° va	neural spiking	IPFC	image identity; location	1	2-5; 25	
[36] Suzuki et al., 1997	rhesus monkey	3	natural images spatial location	DMTS	Identity; 3-8° va	neural spiking	MTL: ERC	image identity; location	1 1-4	6-18; 4	locations are memorized with shapes as context
[37] Spitzer et al., 2014	human	24	tactile flutter	change discrimination	intensity: $\pm 7.3$ % duration: $\pm 150$ ms	EEG $\beta$ power	IPFC ( $\beta$ )	intensity; duration	1	4	source localization; parametric effect; retro-cue
[38] Polanía et al., 2011	human	12	letters	DMTS	identity	EEG time-domain	IPFC; PPC	letter identity	1	2	retro-cue; source localization;
[39] van Kerkoerle et al., 2016	rhesus monkey	2	curves	curve tracing	N/A	neural spiking	VC: V1	location	1	2	
[40] Lundquist et al., 2016	rh. & fascic. monkey	2	colored locations	change detection	N/A	neural spiking	IPFC; FEF	location	2-3	6	content-specificity associated with $\gamma$ -lFP; also location-&-color specificity
[41] Lara & Wallis, 2014	rhesus monkey	3	colored locations	change detection	40-100 $\Delta E$ in color space	neural spiking	IPFC	location	1-2	4	color null effect; IMC
[42] Vicente-Grabovetsky et al., 2012	human	19	grating wedges	change detection	N/A	BOLD	VC: V1-V2	location	2	4	color-cues for encoding; HRF modelling; ROIs; searchlight
[43] Constantinidis & Steinmetz, 1996	rhesus monkey	3	spatial locations	DMTS	$\pm 45^\circ$ ra;	neural spiking	PPC	location	1	8	nonmatching items as distractors
[44] Qi et al., 2010	rhesus monkey	4	spatial location	DMTS	$\pm 180^\circ$ ra; $\pm 10^\circ$ va	neural spiking	IPFC; PPC	location	1	8	two task variants; non-matching items as distractors
[45] Qi et al., 2011	rhesus monkey	3	spatial location	DMTS	$\pm 180^\circ$ ra;	neural spiking	IPFC	location	1	8	

[46] Zhou et al., 2012	rhesus monkey	3	spatial location	DMTS	$\pm 180^\circ$ ra; $\pm 10^\circ$ va	neural spiking	IPFC; PPC	location	1	8	IMC
[47] Sprague et al., 2016	human	6	spatial location	delayed estimation	detailed recall	BOLD	VC: V1-V4; PPC: IPS0-3; FEF	location	2	6	IEM; retro-cue; ROIs
[48] Jerde et al., 2012	human	4	spatial locations	change detection	titrated to threshold	BOLD	PPC: IPS0-3 FEF	location	1	2	shifted delay-period boxcar
[49] Foster et al., 2016	human	15	spatial locations	(a) estimation (b) change det.	(a) recall (b) $\pm 20^\circ$ ra	EEG $\alpha$ power	N/A	location	1	8	IEM; alpha-band specificity
[50] Peters et al., 2015	human	20	spatial locations	switching of attent., match.	$\pm 30^\circ$ ra	BOLD	VC: V1-V4; PPC	location	4 (1)	12	specificity for attended item; ROIs
[51] Sprague et al., 2014	human	4	spatial locations	change detection	$\pm 0.1-1.5^\circ$ ra	BOLD	VC: V1-V4; PPC: IPS0-3; FEF	location	1-2	8	IEM; retro-cue; ROIs
[52] Armstrong et al., 2009	rhesus monkey	2	spatial locations	cue for other task	$\pm 60^\circ$ ra	neural spiking	FEF	location	1	6	
[53] Jacob & Nieder, 2014	rhesus monkey	2	clouds of dots	change detection	$\pm 1-3$ dots	neural spiking	IPFC, PPC: VIP	numerosity	1	4	dot cloud distractor
[54] Ramirez-Cardenas et al., 2016	rhesus monkey	2	clouds of dots	change detection	$\pm 1-4$ dots	neural spiking	IPFC, PPC: VIP	numerosity	1	5	includes zero
[55] Nieder et al., 2004	rhesus monkey	2	clouds of dots	change detection	$\pm 1-4$ dots	neural spiking	PPC: SPL, IPL, IPS	numerosity	1	5	
[56] Nieder et al., 2002	rhesus monkey	2	clouds of dots	change detection	$\pm 1-4$ dots	neural spiking	IPFC	numerosity	1	5	
[57] Spitzer et al., 2014	human	24	vis., tac. & aud. pulses	change discrimination	$\pm 1$ pulse	EEG $\alpha/\beta$ power	IPFC ( $\beta$ ) VC;	numerosity	1	6	source localization; parametric effect
[58] Nieder, 2012	rhesus monkey	2	visual & auditory pulses	change detection	$\pm 1$ pulse	neural spiking	IPFC, PPC: VIP	numerosity	1	4	
[59] Freedman et al., 2001	rhesus monkey	2	cat-dog morphs	DMTC	categorical	neural spiking	IPFC	object category	1	2	intermediate morphs show categorical response
[60] Roy et al., 2010	rhesus monkey	2	cat-dog morphs	DMTC	categorical	neural spiking	IPFC	object category	1	4 (3)	intermediate morphs show categorical response
[61] McKee et al., 2014	rhesus monkey	3	cat-dog morphs	DMTC	categorical	neural spiking	(a) IPFC; (b) IT	object category	1	2 (3)	(a) more categorical (b) less categorical
[62] Freedman et al., 2003	rhesus monkey	3	cat-dog morphs	DMTC	categorical	neural spiking	(a) IPFC; (b) IT	object category	1	2 (3)	(a) more categorical (b) less categorical
[63] Cromer et al., 2010	rhesus monkey	2	cat-dog & car morphs	DMTC	categorical	neural spiking	IPFC	object category	1	4 (3)	intermediate morphs show categorical response
[64] Rainer et al., 1998	rhesus monkey	2	r.-l. objects & their location	DMTS	identity; $\pm 90^\circ$ ra	neural spiking	IPFC	object identity location	1	3; 4	sample object repeated for a block of trials.
[65] Lee & Baker, 2013	human	22	real-life objects	(a) DMTC; (b) detail match	(a) categorical (b) 1/12 <sup>th</sup> of img.	BOLD	(a) IPFC (b) FG	object identity	1	6	retro-cue; ROIs
[66] Rao et al., 1997	rh. & fascic. monkey	2	real-life objects	DMTS	Identity	neural spiking	IPFC	object identity	1	NA	subsequent response-correlated spatial task
[67] Woloszyn & Sheinberg, 2009	rhesus monkey	2	real-life objects	DMTS	identity	neural spiking	IT	object identity	1	7	different forms of distractors
[68] Warden & Miller, 2007	rhesus monkey	2	real-life objects	sequence matching	identity	neural spiking	IPFC	object identity	2	4	
[69] Siegel et al., 2009	rhesus monkey	2	real-life objects	sequence recall	identity	neural spiking	IPFC	object identity	2	4	phase-dependent coding

[70] Warden & Miller, 2010	rhesus monkey	2	real-life objects	sequence recall & DMTS	identity	neural spiking	IPFC	object identity	2	4	task-dependent changes
[71] Salazar et al., 2012	rhesus monkey	2	real-life objects	DMTS	identity	local field potentials	IPFC; PPC	object identity location	1	3	content-specific IPFC-PPC synchronization
[72] Rainer et al., 1999	rhesus monkey	2	real-life objects	DMTS	identity	neural spiking	IPFC	object identity	1	3	
[73] Harrison & Tong, 2009	human	6	gratings	change discrimination	$\pm 3\text{-}6^\circ$ ra	BOLD	VC: V1-V4	orientation	1	2	retro-cues; ROIs
[74] Bettencourt & Xu, 2016	human	10	gratings	change discrimination	$\pm 3\text{-}6^\circ$ ra	BOLD	VC: V1-V4; PPC: sIPS	orientation	1	2	face and house distractors; retro-cue; ROIs
[75] Ester et al., 2009	human	17	gratings	change detection	titrated to threshold	BOLD	VC: V1	orientation	1	2	retro-cue; ROIs
[76] Sneve et al., 2012	human	6	gratings	change discrimination	titrated to threshold	BOLD	VC: V1-V4, LO1	orientation	1	2	retro-cue; ROIs
[77] Ester et al., 2013	human	20	gratings	delayed estimation	detailed recall	BOLD	VC: V1-V2	orientation	1	8	ROIs; IEM
[78] Pratte & Tong, 2014	human	8	gratings	change discrimination	titrated to threshold	BOLD	VC: V1-V4	orientation	2	4	retro-cue; ROIs
[79] Ester et al., 2015	human	6	gratings	delayed estimation	detailed recall	BOLD	VC: V1, V4; FEF; IPFC	orientation	1	9	retro-cue; ROIs; IEM
[80] Wolff et al., 2015	human	24	gratings	change discrimination	$\pm 4\text{-}45^\circ$ ra	EEG time-domain	parieto-occipital electrodes	orientation	1	4	
[81] Albers et al., 2013	human	24	gratings	change discrimination	titrated to threshold	BOLD	VC: V1-V3;	orientation	1	3	retro-cue; ROIs; includes mental rotation task
[82] Serences et al., 2009	human	7	colored gratings	change detection	titrated to threshold	BOLD	VC: V1	orientation; color	1	2	retro-cue; ROIs
[83] Christophel et al., 2012	human	17	color patterns	similarity discrimination	pattern correlation $z < 0.6$	BOLD	VC; PPC	pattern identity	1	4	retro-cue; searchlight
[84] Christophel & Haynes 2014	human	17	motion patterns	similarity discrimination	titrated to threshold	BOLD	hMT+; PPC; SC;	pattern identity	1	8	retro-cue; searchlight
[85] Christophel et al., 2015	human	21	color patterns	similarity discrimination	titrated to threshold	BOLD	VC; PPC	pattern identity rotation	1	12	retro-cue; searchlight; includes mental rotation task
[86] Gottlieb et al., 1989	baboon	1	pure tones	DMTS	N/A	neural spiking	AC	pitch	1	3-4	sample stimuli preselected based on perceptual selectivity
[87] Kumar et al., 2016	human	17	pure tones	change detection	pitch: $\pm 10\%$ Hz	BOLD	AC; IFG (L)	pitch	1	2	retro-cues; ROIs
[88] Linke et al., 2011	human	16	pure tones	change detection	pitch $\pm 1\text{-}3$ semitones	BOLD	AC: HG	pitch	2	4	HRF modelling; ROIs
[89] Christophel et al., 2014	human	44	complex shapes	similarity discrimination	identity	BOLD	LOC; PPC; FEF	shape identity	1	6	retro-cue; searchlight; rotation-invariance
[90] Takeda et al., 2005	rhesus monkey	2	complex shapes	DMTS	identity	neural spiking	IT	shape identity	1	24	nonmatching items as distractors
[91] Miyashita & Chang, 1988	Japanese monkey	2	fractal shapes	DMTS	identity	neural spiking	IT	shape identity	1	8	high degree of symmetry
[92] Meyers et al., 2012	rhesus monkey	2	simple shapes	DMTS	identity	neural spiking	IPFC	shape identity & location	1	8	
[93] Meyer et al., 2011	rhesus monkey	4	simple shapes & locations	DMTS	identity; $\pm 10^\circ$ va	neural spiking	IPFC	shape identity & location	1	8	more spatial information in dorsal PFC

[94] Linke & Cusack, 2015	human	22	natural sounds	Change Detection	altered frequency, speed or loudness	BOLD	AC: HG; MTG	sound identity	1	12	HRF modelling: ROIs; see their Fig. 2 for details
[95] Eiselt & Nieder, 2015	rhesus monkey	2	gratings, lines, clouds of dots	change detection	x.5-x2 cpd; x.6-x1.7° va; x.33-x2 #	neural spiking	IPFC	sp. frequency, length, number	1	3	
[96] Hussar & Pasternak, 2013	rhesus monkey	2	motion flow fields	change detection	direct.: ±10-90° ra speed: x0.1-x3	neural spiking	IPFC	speed	1	2	
[97] Zhou & Fuster, 1996	rhesus monkey	2	haptic surface textures	DMTS	identity	neural spiking	SC	surface texture	1	2	

**Supplementary Table S1, related to Figure 1. Studies reporting persistent stimulus-selective activity in humans and non-human primates.** Data from delay-periods during which subjects can prepare a specific motor output (e.g. delayed response tasks) and tasks that involve any form of mental transformation or explicitly learned association are excluded. Studies contrasting high-level categories (object vs. spatial, faces vs. houses) are omitted. **Species** identifies the species. **N** names the number of individual subjects. **Stimuli** names the type of stimulus used. **Task Type** identifies the type of task during which content-specificity was found. DMTS = delayed match-to-sample; DMTC = delayed match-to-category; DMTA = delayed match-to-association. **Task Precision** reports the level of precision required by the subject to perform in the task. If available numerical estimates of task difficulty (e.g. how much a grating was rotated during a change discrimination task) are reported. ‘Titrated to threshold’ signifies procedures during which the difficulty was adapted to the ability of the individual subject to perform the task (e.g. using a staircase procedure). ‘Identity’ is used as a label for studies that use clearly distinct stimuli (e.g. a different object) as foils. ‘Categorical’ signifies tasks that necessitate the generalization from a single stimulus to a category. Please note the difference to larger-level categories sometimes used in human imaging work (e.g. house, faces) specificity for which is not covered here. cpd = cycle per degree; ra = radial angle; va = visual angle; **Signal** reports the type of signal for which content-specificity is reported. **Brain Areas** names the areas showing significant delay-period content-specificity are reported. AC = auditory cortex; ERC = entorhinal cortex; FEF = frontal eye fields; HG = Heschl’s gyrus; hMT+ = human analog to MT/MST; IFG: inferior frontal gyrus; IOS = intraoccipital sulcus; IPL = inferior parietal lobule; IPS = intraparietal sulcus; IT = inferior temporal cortex; IIPC = lateral intraparietal cortex; LIP = lateral intraparietal area; LOC = lateral occipital complex; IPFC = lateral prefrontal cortex; MPM = medial premotor cortex; MTG = middle temporal gyrus; MTL = medial temporal lobe; POC = parietooccipital cortex; PM = premotor cortex; PPC = posterior parietal cortex; SC = somatosensory cortex; sIPS = superior intraparietal sulcus; VC = visual cortex; VIP = ventral intraparietal area; (L) = Left; (R) = Right; **Specificity** names the type(s) of information for which the study showed delay-period content-specific neural responses independently of the response. **N of Contents per Trial** identifies the number of items memorized in each trial. Brief memorization during retro-cue procedures are disregarded. Number of elements are reported for sequences and multi-item displays. **N of Contents per Analysis** identifies the number of contents (stimuli or categories) differentiated in the analyses of neural data for each individual unit e.g. (voxels, cells) within each subject. Numbers in brackets give number of stimuli per category if applicable. **Notes.** IEM = inverse encoding model; IMC = inverse memory codes; ROI = region-of-interest; HRF = hemodynamic response function; Order determined alphabetically by specificity and species.

## References

- 1 Buschman, T.J. *et al.* (2011) Neural substrates of cognitive capacity limitations. *Proc. Natl. Acad. Sci. USA* 108, 11252–11255
- 2 Fuster, J. and Jervey, J. (1981) Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. *Science* 212, 952–955
- 3 Fuster, J.M. and Jervey, J.P. (1982) Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. *J. Neurosci.* 2, 361–375
- 4 Fuster, J.M. (1990) Inferotemporal units in selective visual attention and short-term memory. *J. Neurophysiol* 64, 681–697
- 5 Xing, Y. *et al.* (2013) Decoding Working Memory of Stimulus Contrast in Early Visual Cortex. *J. Neurosci.* 33, 10301–10311
- 6 Riggall, A.C. and Postle, B.R. (2012) The Relationship between Working Memory Storage and Elevated Activity as Measured with Functional Magnetic Resonance Imaging. *J. Neurosci.* 32, 12990–12998
- 7 Emrich, S.M. *et al.* (2013) Distributed Patterns of Activity in Sensory Cortex Reflect the Precision of Multiple Items Maintained in Visual Short-Term Memory. *J. Neurosci.* 33, 6516–6523
- 8 Swaminathan, S.K. *et al.* (2013) A Comparison of Lateral and Medial Intraparietal Areas during a Visual Categorization Task. *J. Neurosci.* 33, 13157–13170
- 9 Rishel, C.A. *et al.* (2013) Independent Category and Spatial Encoding in Parietal Cortex. *Neuron* 77, 969–979
- 10 Bisley, J.W. *et al.* (2004) Activity of neurons in cortical area MT during a memory for motion task. *J. Neurophysiol.* 91, 286–300
- 11 Zaksas, D. and Pasternak, T. (2006) Directional signals in the prefrontal cortex and in area MT during a working memory for visual motion task. *J. Neurosci.* 26, 11726–11742
- 12 Mendoza-Halliday, D. *et al.* (2014) Sharp emergence of feature-selective sustained activity along the dorsal visual pathway. *Nat. Neurosci.* 17, 1255–1262
- 13 Hussar, C.R. and Pasternak, T. (2012) Memory-Guided Sensory Comparisons in the Prefrontal Cortex: Contribution of Putative Pyramidal Cells and Interneurons. *J. Neurosci.* 32, 2747–2761
- 14 Wimmer, K. *et al.* (2016) Transitions between Multiband Oscillatory Patterns Characterize Memory-Guided Perceptual Decisions in Prefrontal Circuits. *J. Neurosci.* 36, 489–505
- 15 Sarma, A. *et al.* (2016) Task-specific versus generalized mnemonic representations in parietal and prefrontal cortices. *Nat Neurosci* 19, 143–149
- 16 Lemus, L. *et al.* (2009) Neural encoding of auditory discrimination in ventral premotor cortex. *PNAS* 106, 14640–14645

- 17 Vergara, J. *et al.* (2016) A Neural Parametric Code for Storing Information of More than One Sensory Modality in Working Memory. *Neuron* 89, 54–62
- 18 Spitzer, B. *et al.* (2010) Oscillatory Correlates of Vibrotactile Frequency Processing in Human Working Memory. *J. Neurosci.* 30, 4496–4502
- 19 Spitzer, B. and Blankenburg, F. (2011) Stimulus-dependent EEG activity reflects internal updating of tactile working memory in humans. *Proc. Natl. Acad. Sci. USA* 108, 8444–8449
- 20 Romo, R. *et al.* (1999) Neuronal correlates of parametric working memory in the prefrontal cortex. *Nature* 399, 470–473
- 21 Brody, C.D. *et al.* (2003) Timing and Neural Encoding of Somatosensory Parametric Working Memory in Macaque Prefrontal Cortex. *Cereb. Cortex* 13, 1196–1207
- 22 Barak, O. *et al.* (2010) Neuronal Population Coding of Parametric Working Memory. *J. Neurosci.* 30, 9424–9430
- 23 Hernández, A. *et al.* (2002) Temporal Evolution of a Decision-Making Process in Medial Premotor Cortex. *Neuron* 33, 959–972
- 24 Hernández, A. *et al.* (2010) Decoding a Perceptual Decision Process across Cortex. *Neuron* 66, 300–314
- 25 Romo, R. *et al.* (2002) Neuronal correlates of decision-making in secondary somatosensory cortex. *Nat Neurosci* 5, 1217–1225
- 26 Salinas, E. *et al.* (2000) Periodicity and Firing Rate As Candidate Neural Codes for the Frequency of Vibrotactile Stimuli. *J. Neurosci.* 20, 5503–5515
- 27 Spitzer, B. and Blankenburg, F. (2012) Supramodal Parametric Working Memory Processing in Humans. *J. Neurosci.* 32, 3287–3295
- 28 Chelazzi, L. *et al.* (2001) Responses of Neurons in Macaque Area V4 During Memory-guided Visual Search. *Cereb. Cortex* 11, 761–772
- 29 Miller, E.K. *et al.* (1993) Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *J. Neurosci.* 13, 1460–1478
- 30 Chelazzi, L. *et al.* (1998) Responses of Neurons in Inferior Temporal Cortex During Memory-Guided Visual Search. *Journal of Neurophysiology* 80, 2918–2940
- 31 Chelazzi, L. *et al.* (1993) A neural basis for visual search in inferior temporal cortex. *Nature* 363, 345–347
- 32 Miller, E.K. *et al.* (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.* 16, 5154–5167
- 33 Asaad, W.F. *et al.* (2000) Task-specific neural activity in the primate prefrontal cortex. *Journal of Neurophysiology* 84, 451–459
- 34 Hayden, B.Y. and Gallant, J.L. (2013) Working Memory and Decision Processes in Visual Area V4. *Front. Neurosci.* 7, 18
- 35 Rainer, G. *et al.* (1998) Memory fields of neurons in the primate prefrontal cortex. *PNAS* 95, 15008–15013
- 36 Suzuki, W.A. *et al.* (1997) Object and Place Memory in the Macaque Entorhinal Cortex. *J. Neurophysiol.* 78, 1062–1081
- 37 Spitzer, B. *et al.* (2014) Working memory coding of analog stimulus properties in the human prefrontal cortex. *Cereb. Cortex* 24, 2229–2236
- 38 Polanía, R. *et al.* (2011) Noninvasively Decoding the Contents of Visual Working Memory in the Human Prefrontal Cortex within High-gamma Oscillatory Patterns. *Journal of Cognitive Neuroscience* 24, 304–314
- 39 van Kerkoerle, T. *et al.* (in press) The influence of attention and working memory on neuronal activity in the different layers of primary visual cortex. *Nat. Commun.*
- 40 Lundqvist, M. *et al.* (2016) Gamma and Beta Bursts Underlie Working Memory. *Neuron* 90, 152–164
- 41 Lara, A.H. and Wallis, J.D. (2014) Executive control processes underlying multi-item working memory. *Nat. Neurosci.* 17, 876–883
- 42 Vicente-Grabovetsky, A. *et al.* (2012) Strength of Retinotopic Representation of Visual Memories is Modulated by Strategy. *Cereb. Cortex* DOI: 10.1093/cercor/bhs313
- 43 Constantinidis, C. and Steinmetz, M.A. (1996) Neuronal activity in posterior parietal area 7a during the delay periods of a spatial memory task. *J. Neurophysiol.* 76, 1352–1355
- 44 Qi, X.-L. *et al.* (2010) Comparison of neural activity related to working memory in primate dorsolateral prefrontal and posterior parietal cortex. *Front. Syst. Neurosci.* 4, 12
- 45 Qi, X.-L. *et al.* (2011) Changes in Prefrontal Neuronal Activity after Learning to Perform a Spatial Working Memory Task. *Cereb. Cortex* DOI: 10.1093/cercor/bhr058
- 46 Zhou, X. *et al.* (2012) Neurons with inverted tuning during the delay periods of working memory tasks in the dorsal prefrontal and posterior parietal cortex. *J. Neurophysiol.* 108, 31–38
- 47 Sprague, T.C. *et al.* (2016) Restoring Latent Visual Working Memory Representations in Human Cortex. *Neuron* 91, 694–707
- 48 Jerde, T.A. *et al.* (2012) Prioritized Maps of Space in Human Frontoparietal Cortex. *J. Neurosci.* 32, 17382–17390
- 49 Foster, J.J. *et al.* (2016) The topography of alpha-band activity tracks the content of spatial working memory. *Journal of Neurophysiology* 115, 168–177
- 50 Peters, B. *et al.* (2015) Activity in Human Visual and Parietal Cortex Reveals Object-Based Attention in Working Memory. *J. Neurosci.* 35, 3360–3369
- 51 Sprague, T.C. *et al.* (2014) Reconstructions of Information in Visual Spatial Working Memory Degrade with Memory Load. *Curr. Biol.* 24, 2174–2180
- 52 Armstrong, K.M. *et al.* (2009) Selection and Maintenance of Spatial Information by Frontal Eye Field Neurons. *J. Neurosci.* 29, 15621–15629
- 53 Jacob, S.N. and Nieder, A. (2014) Complementary Roles for Primate Frontal and Parietal Cortex in Guarding Working Memory from Distractor Stimuli. *Neuron* 83, 226–237
- 54 Ramirez-Cardenas, A. *et al.* (2016) Neuronal Representation of Numerosity Zero in the Primate Parieto-Frontal Number Network. *Current Biology* 26, 1285–1294
- 55 Nieder, A. and Miller, E.K. (2004) A parieto-frontal network for visual numerical information in the monkey. *Proc. Natl. Acad. Sci. USA* 101, 7457–7462
- 56 Nieder, A. *et al.* (2002) Representation of the Quantity of Visual Items in the Primate Prefrontal Cortex. *Science* 297, 1708–1711
- 57 Spitzer, B. *et al.* (2014) Parametric Alpha- and Beta-Band Signatures of Supramodal Numerosity Information in Human Working Memory. *J. Neurosci.* 34, 4293–4302
- 58 Nieder, A. (2012) Supramodal numerosity selectivity of neurons in primate prefrontal and posterior parietal cortices. *Proc. Natl. Acad. Sci. USA* 109, 11860–11865
- 59 Freedman, D.J. *et al.* (2001) Categorical representation of visual stimuli in the primate prefrontal cortex. *Science* 291, 312–316
- 60 Roy, J.E. *et al.* (2010) Prefrontal Cortex Activity during Flexible Categorization. *J. Neurosci.* 30, 8519–8528

- 61 McKee, J.L. *et al.* (2014) Task Dependence of Visual and Category Representations in Prefrontal and Inferior Temporal Cortices. *J. Neurosci.* 34, 16065–16075
- 62 Freedman, D.J. *et al.* (2003) A Comparison of Primate Prefrontal and Inferior Temporal Cortices during Visual Categorization. *J. Neurosci.* 23, 5235–5246
- 63 Cromer, J.A. *et al.* (2010) Representation of Multiple, Independent Categories in the Primate Prefrontal Cortex. *Neuron* 66, 796–807
- 64 Rainer, G. *et al.* (1998) Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature* 393, 577–578
- 65 Lee, S.-H. *et al.* (2013) Goal-dependent dissociation of visual and prefrontal cortices during working memory. *Nat. Neurosci.* 16, 997–999
- 66 Rao, S.C. *et al.* (1997) Integration of what and where in the primate prefrontal cortex. *Science* 276, 821–824
- 67 Woloszyn, L. and Sheinberg, D.L. (2009) Neural dynamics in inferior temporal cortex during a visual working memory task. *J. Neurosci.* 29, 5494–5507
- 68 Warden, M.R. and Miller, E.K. (2007) The representation of multiple objects in prefrontal neuronal delay activity. *Cerebral Cortex* 17, i41–i50
- 69 Siegel, M. *et al.* (2009) Phase-dependent neuronal coding of objects in short-term memory. *Proc. Natl. Acad. Sci. USA* 106, 21341–21346
- 70 Warden, M.R. and Miller, E.K. (2010) Task-Dependent Changes in Short-Term Memory in the Prefrontal Cortex. *The Journal of Neuroscience* 30, 15801–15810
- 71 Salazar, R.F. *et al.* (2012) Content-Specific Fronto-Parietal Synchronization During Visual Working Memory. *Science* 338, 1097–1100
- 72 Rainer, G. *et al.* (1999) Prospective Coding for Objects in Primate Prefrontal Cortex. *J. Neurosci.* 19, 5493–5505
- 73 Harrison, S.A. and Tong, F. (2009) Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458, 632–635
- 74 Bettencourt, K.C. and Xu, Y. (2016) Decoding the content of visual short-term memory under distraction in occipital and parietal areas. *Nat. Neurosci.* 19, 150–157
- 75 Ester, E.F. *et al.* (2009) Spatially global representations in human primary visual cortex during working memory maintenance. *J. Neurosci.* 29, 15258–15265
- 76 Sneve, M.H. *et al.* (2012) Visual short-term memory: Activity supporting encoding and maintenance in retinotopic visual cortex. *Neuroimage* 63, 166–178
- 77 Ester, E.F. *et al.* (2013) A Neural Measure of Precision in Visual Working Memory. *J. Cogn. Neurosci.* 25, 754–761
- 78 Pratte, M.S. and Tong, F. (2014) Spatial specificity of working memory representations in the early visual cortex. *J. Vis.* 14, 22
- 79 Ester, E.F. *et al.* (2015) Parietal and Frontal Cortex Encode Stimulus-Specific Mnemonic Representations during Visual Working Memory. *Neuron* 87, 893–905
- 80 Wolff, M.J. *et al.* (2015) Revealing hidden states in visual working memory using electroencephalography. *Front Syst Neurosci* 9,
- 81 Albers, A.M. *et al.* (2013) Shared Representations for Working Memory and Mental Imagery in Early Visual Cortex. *Curr. Biol.* 23, 1427–1431
- 82 Serences, J.T. *et al.* (2009) Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* 20, 207–214
- 83 Christophel, T.B. *et al.* (2012) Decoding the Contents of Visual Short-Term Memory from Human Visual and Parietal Cortex. *J. Neurosci.* 32, 12983–12989
- 84 Christophel, T.B. and Haynes, J.-D. (2014) Decoding complex flow-field patterns in visual working memory. *Neuroimage* 91, 43–51
- 85 Christophel, T.B. *et al.* (2015) Parietal and early visual cortices encode working memory content across mental transformations. *Neuroimage* 106, 198–206
- 86 Gottlieb, Y. *et al.* (1989) Single unit activity in the auditory cortex of a monkey performing a short term memory task. *Exp. Brain Res.* 74, 139–148
- 87 Kumar, S. *et al.* (2016) A Brain System for Auditory Working Memory. *J. Neurosci.* 36, 4492–4505
- 88 Linke, A.C. *et al.* (2011) Stimulus-specific suppression preserves information in auditory short-term memory. *Proc. Natl. Acad. Sci. USA* 108, 12961–12966
- 89 Christophel, T. *et al.* (2013) Decoding invariant representations in visual working memory. *Journal of Vision* 13, 927–927
- 90 Takeda, M. *et al.* (2005) Active Maintenance of Associative Mnemonic Signal in Monkey Inferior Temporal Cortex. *Neuron* 48, 839–848
- 91 Miyashita, Y. and Chang, H.S. (1988) Neuronal correlate of pictorial short-term memory in the primate temporal cortex. *Nature* 331, 68–70
- 92 Meyers, E.M. *et al.* (2012) Incorporation of new information into prefrontal cortical activity after learning working memory tasks. *Proc. Natl. Acad. Sci. U.S.A.* 109, 4651–4656
- 93 Meyer, T. *et al.* (2011) Stimulus Selectivity in Dorsal and Ventral Prefrontal Cortex after Training in Working Memory Tasks. *J. Neurosci.* 31, 6266–6276
- 94 Linke, A.C. and Cusack, R. (2015) Flexible Information Coding in Human Auditory Cortex during Perception, Imagery, and STM of Complex Sounds. *Journal of Cognitive Neuroscience* DOI: 10.1162/jocn\_a\_00780
- 95 Eiselt, A.-K. and Nieder, A. (2015) Single-cell coding of sensory, spatial and numerical magnitudes in primate prefrontal, premotor and cingulate motor cortices. *Exp Brain Res* 234, 241–254
- 96 Hussar, C.R. and Pasternak, T. (2013) Common Rules Guide Comparisons of Speed and Direction of Motion in the Dorsolateral Prefrontal Cortex. *J. Neurosci.* 33, 972–986
- 97 Zhou, Y.D. and Fuster, J.M. (1996) Mnemonic neuronal activity in somatosensory cortex. *Proc. Natl. Acad. Sci. USA* 93, 10533–10537