fMRI Evidence for Modality-Specific Processing of Conceptual Knowledge on Six Modalities

Simmons, W.K.[1], Pecher, D.[2], Hamann, S.B.[1], Zeelenberg, R.[3], & Barsalou, L.W.[1]

[1]Emory University, [2]Erasmus University Rotterdam, [3]Indiana University

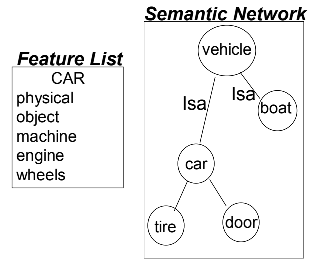
Abstract

Traditional theories assume that amodal representations, such as feature lists and semantic networks, represent conceptual knowledge about the world. According to this view, the sensory, motor, and introspective states that arise during perception and action are irrelevant to representing knowledge. Instead the conceptual system lies outside modality-specific systems and operates according to different principles. Increasingly, however, researchers report that modality-specific systems become active during purely conceptual tasks, suggesting that these systems play central roles in representing knowledge (for a review, see Martin, 2001, Handbook of Functional Neuroimaging of Cognition). In particular, researchers report that the visual system becomes active while processing visual properties, and that the motor system becomes active while processing action properties. The present study corroborates and extends these findings. During fMRI, subjects verified whether or not properties could potentially be true of concepts (e.g., BLENDER-loud). Subjects received only linguistic stimuli, and nothing was said about using imagery. Highly related false properties were used on false trials to block word association strategies (e.g., BUFFALO-winged). To assess the full extent of the modality-specific hypothesis, properties were verified on each of six modalities. Examples include GEMSTONE-glittering (vision), BLENDER-loud (audition), FAUCET-turned (motor), MARBLE-cool (touch), CUCUMBER-bland (taste), and SOAP-perfumed (smell). Neural activity during property verification was compared to a lexical decision baseline. For all six sets of the modality-specific properties, significant activation was observed in the respective neural system. Finding modality-specific processing across six modalities contributes to the growing conclusion that knowledge is grounded in modality-specific systems of the brain.

Background

Amodal Theories

Traditional theories assume that conceptual knowledge is stored separate and apart from the sensory-motor systems through which it was acquired. These accounts employ amodal representations, such as feature lists and semantic networks, to perform conceptual processing.



Modality-Specific Theories

Alternatively, knowledge may be stored in the particular sensory-motor systems that support perception and action with a concept's referents. Thus, modality-specific accounts propose that conceptual processing utilizes representations in the brain's sensory-motor systems. As sensory-motor representations become active during perception and action, association areas capture these representations, and partially reenact them later to represent knowledge (e.g., Barsalou, 1999; Damasio, 1989; Simmons & Barsalou, in press).

Accumulating behavioral and neuroimaging evidence supports this view. For reviews of behavioral evidence, see Barsalou, Simmons, Barbey, & Wilson (2003), Barsalou (in press), and Barsalou, Niedenthal, Barbey, & Ruppert (in press). For reviews of neuroimaging evidence, see Martin (2001) and Martin & Chao (2001)

Of interest to the study reported here are the previous results of Pecher, Zeelenberg, and Barsalou (2003, in press).

Rationale and method of these previous studies

Psychophysical research shows that humans are slower to detect a *current* stimulus when the *preceding* stimulus occurred on a different sensory modality (e.g., switching from vision to audition). This "switching cost" is thought to represent the extra time necessary to switch attention from one sensory-motor modality to another (e.g., Spence, Nicholls, & Driver, 2000). If sensory-motor systems underlie conceptual knowledge, switching costs should be observed in an analogous conceptual task. Thus participants in the Pecher et al. studies were asked to verify properties of concepts that could reside on the same vs. a different modality (e.g., an auditory property preceded by another auditory property vs. a visual property).

Results from these previous studies

Participants were slower to verify a concept's property when the preceding trial's property was on a different sensory-motor modality. Provides evidence that sensory-motor systems become engaged during property verification.

Question: ***Is performing the property verification task associated with property-dependant activation of modality-specific systems in the brain?***

Method

Participants

12 right-handed Emory University undergraduates and community volunteers.

Property Verification Task

- Participants performed the property verification task while undergoing fMRI.
- Trials were blocked by property modality.
- Participants determined whether each property was true or false of its respective category, with half the properties in a block true, and half false.
- In two additional blocks, participants performed a lexical decision task, used as the baseline for later subtractions.
- Different numbers of blocks were performed for each property type, because more properties were available for some modalities than for others (e.g., vision relative to taste). The number of blocks for each modality was 6 for vision and motor, 5 for sound, 2 for touch, taste, and 1 for taste.
- 3 seconds per trial, 8 trials per block, 2 runs
- Participants' response times were collected with a serial response box.

Examples of blocks

Condition	Stimulus
Motor	SACK can be DRAGGED
Motor	SOCK can be UNTIED
Motor	STICK can be FLUNG
Motor	COMPUTER MONITOR can be TORN
Motor	TEST TUBE can be DISENTANGLED
Motor	ROCK can be HURLED
Motor	LAWNMOWER can be PUSHED
Motor	PHOTO can be CARVED
Smell	ASHTRAY can be FRAGRANT
Smell	TAR can be STINKY
Smell	VANILLA can be STENCHY
Smell	WHISKEY can be ODOROUS
Smell	OLD BOOK can be MUSTY
Smell	GARLIC can be PUNGENT
Smell	INCENSE can be SCENTLESS
Smell	SKUNK can be PERFUMED
Sound	POODLE can be MEOWING
Sound	BEES can be BUZZING
Sound	RICE CRISPIES can be CRACKLING
Sound	LEAVES can be RUSTLING
Sound	KEYS can be JINGLING
Sound	ANT can be SQUEALING
Sound	FLOORBOARDS can be CREAKING
Sound	MOOSE can be GIGGLING
Taste	MUFFIN can be STALE
Taste	BISCUIT can be ACIDIC
Taste	TABASCO can be BLAND
Taste	CRANBERRIES can be TART
Taste	SALSA can be SPICY
Taste	MUSTARD can be TANGY
Taste	MARGARINE can be SHARP
Taste	LEMON can be BRINY
Taste	SOUP can be SALTY
Touch	RUBBER can be SLIPPERY
Touch	MARBLE can be COOL
Touch	LEMONADE can be DRY
Touch	SAUNA can be CHILLY
Touch	POPSICLE can be HOT
Touch	PEANUT BUTTER can be STICKY
Touch	HAT can be FEVERISH
Touch	BLANKET can be ITCHY
Visual	CROW can be BLOND
Visual	ELEPHANT can be ORANGE
Visual	RUBBER DUCK can be YELLOW
Visual	WINE can be SPECKLED
Visual	WOMAN can be BRUNETTE
Visual	TENNIS BALL can be GLOSSY
Visual	GEMSTONE can be GLITTERING
Visual	FLAG can be STRIPED

FMRI Methods

- Image acquisition
  - Gradient recalled echo MRI
  - 1.5 T Philips Intera scanner
  - TR = 3000ms
  - TE = 40ms
  - 24 axial slices (5 mm)
- Image Processing
  - SPM realignment
  - Spatial smoothing using an 8mm isotropic Gaussian kernel
  - Image analyses in SPM99

Results

Behavioral data

- No RT differences among property modalities ($F_{5,1544}$ =.881 , p=.493).
- Property verification slower than lexical decision ($F_{1,1692}$ = 204.57, p <0.000).

Descriptive Statistics for Behavioral RT Data
(*Correct responses only*)

	Mean	Std Deviation	Median	Count
Visual	1412	324	1335	389
Auditory	1406	288	1344	312
Motor	1429	306	1360	383
Touch	1423	340	1353	129
Taste	1407	315	1337	128
Smell	1470	304	1388	62
Lexical decision	1020	252	953	141

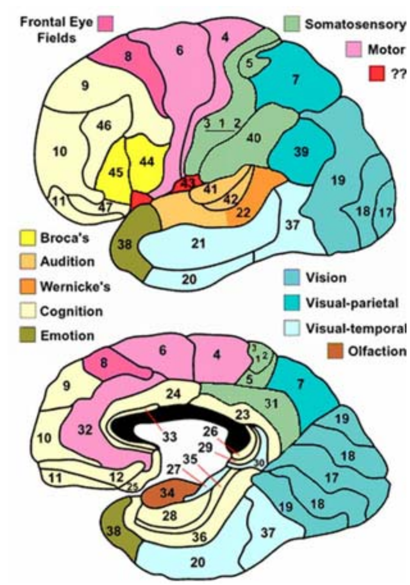
Imaging data

Property blocks. Brain activations for a given type of property were averaged across all blocks for that property type.

Baseline task and subtraction. Brain activations were average across lexical decision blocks. Activity for lexical decision was then subtracted from the average activity for each property type (e.g., visual property verification minus lexical decision). Subtracting the lexical decision task removed activation due to processing of word forms, leaving activation for conceptual processing.

Analyses. Results reported here are from random effects analyses (uncorrected p < 0.001, spatial extent = 7 voxels). The same pattern of results was obtained using other designs.

Assigning activations to sensory-motor areas in the brain. Significant voxel clusters were assigned to specific Brodmann areas with the aid of MRIcro. Brodmann area activations were then assigned to the visual, auditory, motor, and somatosensory systems using the maps to the right.



The brain localizations of olfactory and gustatory areas are difficulty to define. Widely-agreed upon Brodmann assignments are not available (Zald & Pardo, 2000). For this reason, activations were assigned to the olfactory and gustatory systems on the bases of proximity to activations observed in previous imaging studies (Sobel, et al., 2000; Zald & Pardo, 2000). The frontal operculum was defined as primary gustatory cortex. The piriform cortex was defined as primary olfactory cortex (no activations were found in this area). Secondary gustatory and secondary olfactory cortices were defined as orbito-frontal cortex near ±20, 40, -10.

Voxel Counts

Assessing the original hypothesis

The original prediction was that the trials for each property type would activate its respective modality-specific area (the main diagonal in the figure below). As can be seen, such areas were indeed active. Activation, however, was not strictly confined to the target property's modality. Instead, sensory-motor activity was always multi-modal, activating multiple modalities. Multiple modalities were active for every property type.

Voxel counts

	Sensory-Motor Area					
Contrast	Vision	Sound	Motor	Touch	Taste	Smell
Vision - lexdec	51	0	11	32	27	16
Sound - lexdec	296	13	17	39	0	0
Motor - lexdec	81	0	8	36	0	0
Touch - lexdec	146	0	26	9	0	0
Taste - lexdec	948	0	50	13	24	24
Smell - lexdec	66	0	54	75	12	0

An alternative hypothesis

On every trial, participants processed both a property *and* a concept. Even though the properties were blocked by sensory-motor modality, the concepts almost certainly refer to referents that are experienced on multiple modalities. Perhaps activity in sensory-motor areas was driven, not only by the property, but also by the multi-modal concept that preceded it.

****** If so, then peoples' multi-modal experience of the concepts and properties in a block should predict the distribution of brain activations across sensory-motor modalities. ******

Scaling Study

To assess this hypothesis, a separate scaling study was undertaken. Independent participants rated how much they experienced the concepts and properties on the six sensory-motor modalities.

Scaling Method

Twelve participants (not in the imaging study) rated the concepts and properties separately for how much each is experienced on the six sensory-motor modalities. Half rated the concepts first, and half rated the properties first. Participants used a 0 to 6 scale, with 0 meaning that a concept or property was completely uninvolved in the experience, and with 6 meaning complete involvement. The rating frames were:

"When you experience an X (where X could be a concept or property):

How much of your experience involves SEEING it?
How much of your experience involves HEARING it?
How much of your experience involves ACTING ON it?
How much of your experience involves FEELING it?
How much of your experience involves TASTING it?
How much of your experience involves SMELLING it?

Scaling Results

The six average scale values for each concept were averaged for all concepts used to test a particular property type (e.g., all concepts used to assess motor properties were averaged). The overall averages for each property type established a sensory-motor profile for the concepts used to test it. These profiles are shown below. As can be seen, the concepts used to test the different property types differed in their sensory-motor profiles.

Concept Ratings

	Sensory-motor modality					
Property Block	**vision**	**sound**	**motor**	**touch**	**taste**	**smell**
Visual	5.18	1.61	2.36	2.85	1.32	2.20
Sound	5.15	4.02	3.18	3.05	0.74	1.27
Motor	5.05	1.71	3.39	3.69	1.25	1.88
Touch	5.07	1.74	3.14	4.01	2.38	2.85
Taste	4.61	0.46	2.74	2.28	5.69	4.17
Smell	4.34	0.69	2.32	2.10	2.30	5.07

The six average scale values for each property were averaged for all properties used to test a particular property type (e.g., all motor properties were averaged). The overall averages for each property type established a sensory-motor profile for the properties tested. These profiles are shown below. As can be seen, the different property types differed in their sensory-motor profiles.

Property Ratings

	Sensory-motor modality					
Property Block	**vision**	**sound**	**motor**	**touch**	**taste**	**smell**
Visual	5.61	0.39	0.71	1.29	0.33	0.53
Sound	2.98	5.71	1.70	1.61	0.16	0.26
Motor	5.13	2.82	2.32	2.53	0.42	0.36
Touch	3.55	0.72	2.49	5.29	1.42	1.22
Taste	2.22	0.49	1.81	1.99	4.63	3.22
Smell	1.46	0.17	1.63	1.01	1.58	5.28

Using the Concept and Property Ratings to Predict the Voxel Counts

To assess whether the concepts, properties, or both, predicted the multi-modal brain activations in the property verification task, a series of regression analyses were performed. Before these analyses could be conducted, however, a natural log transformation was applied to the voxel count data to normalize the distribution. Next, the natural log transformed voxel counts were regressed on to the concept and property ratings.

Individual regressions for concept and property ratings. To assess the individual abilities of the concept ratings and property ratings to predict the voxel counts, an independent regression for each rating type was performed.

Rating Type	B	SE B	β	*r*	R^2	*p*
Concept	.85	.18	.63	.63	.40	.000
Property	.41	.18	.36	.36	.13	.03

Surprisingly, the concept ratings explained the voxel counts better than the property ratings! Whereas the concept ratings accounted for 40% of the variance in the voxel counts ($F_{1,34} = 22.7$, $p<0.000$), the properties only accounted for 13% ($F_{1,34} = 5.05$, $p<0.05$). This suggests that processing the concepts contributed more to the observed brain activations than processing the properties. The sensory-motor profiles for the concepts used to test each property type were most responsible for brain activation.

Joint regression for concept and property ratings. To assess the joint ability of the concept ratings and the property ratings to predict the voxel counts, a multiple regression with both rating types was performed.

Rating Type	B	SE B	β	*r*	R^2	*p*
Overall Model				.70	.49	.000
Concept	1.42	.30	1.06			.000
Property	-.59	.25	-.52			.027

Together, the concept ratings and property ratings exhibited a multiple correlation of .70 with the voxel counts, and explained nearly half the variance ($F_{2,33} = 15.53$, $p<0.000$). This suggests that multi-modal content of the concepts and properties together determined the multi-modal patterns of activation observed during property verification.

Conclusions

- Brain activation during property verification did not solely reflect the properties being processed. The dominant brain activation for each property type did not reside solely in its respective modality. On trials with motor properties, for example, not just motor areas were active.

- Instead, each type of property trial produced multi-modal activation, where the multi-modal profile differed by property type. Rather than being restricted to the modality of the property, neural activity was multi-modal.

- Independent scaling of the concepts and properties established their sensory-motor profiles. In turn, these profiles predicted the multi-modal patterns of brain activation during property verification, with a correlation of .70, explaining 49% of the variance.

- Although the multi-modal profiles for both the concepts and properties both predicted the voxel counts significantly, the concept profiles were more important than the property profiles. This suggests that processing the concepts dominated brain activation relative to processing the properties.

- These results support modality-specific accounts of knowledge representation (e.g., Damasio, 1989; Barsalou, 1999; Martin, 2001). By this account, performing a property verification trial activates perceptual simulations for both the trial's concept and its property. The activation observed in sensory-motor systems reflects the multi-modal simulations required to represent the multi-modal content of the concept and the property.

References

Barsalou, L.W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*, 577-660.

Barsalou, L.W. (in press). Situated simulation in the human conceptual system. *Language and Cognitive Processes.*

Barsalou, L.W., Niedenthal, P.M., Barbey, A., & Ruppert, J. (in press). Social embodiment. In B. Ross (Ed.), *The Psychology of Learning and Motivation*, Vol. 43. San Diego: Academic Press.

Barsalou, L.W., Simmons, W.K., Barbey, A.K., & Wilson, C.D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences, 7,* 84-91.

Damasio, A.R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition, 33,* 25-62.

Martin, A. (2001). Functional neuroimaging of semantic memory. In Cabeza R & Kingstone A (Eds), *Handbook of Functional NeuroImaging of Cognition* (pp.153-186). Cambridge: MIT Press.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: structure and processes. *Current Opinion in Neurobiology, 11,* 194-201.

Pecher, D., Zeelenberg, R., & Barsalou, L.W. (2003). Verifying different–modality properties for concepts produces switching costs. *Psychological Science, 14,* 119-125.

Pecher, D., Zeelenberg, R., & Barsalou, L.W. (in press). Sensorimotor simulations underlie conceptual representations: Modality-specific effects of prior activation. *Psychonomic Bulletin & Review*.

Simmons, K., & Barsalou, L.W. (in press). The similarity-in-topography principle: Reconciling theories of conceptual deficits. *Cognitive Neuropsychology*.

Sobel, N., Prabhakaran, V., Zhao, Z., Desmond, JE., Glover, GH., Sullivan, EV., Gabrieli, JD. (2000). Time course of odorant-induced activation in the human primary olfactory cortex. *Journal of Neurophysiology, 83,* 537-551.

Solomon, K.O., & Barsalou, L.W. (2001). Representing properties locally. *Cognitive Psychology, 43,* 129-169.

Spence, C., Nicholls, M. E. R., & Driver, J. (2000). The cost of expecting events in the wrong sensory modality. *Perception & Psychophysics, 63,* 330-336.

Zald, D.H. & Pardo, J.V. (2000). Functional neuroimaging of the olfactory system in humans. *International Journal of Psychophysiology, 36,* 165-181.

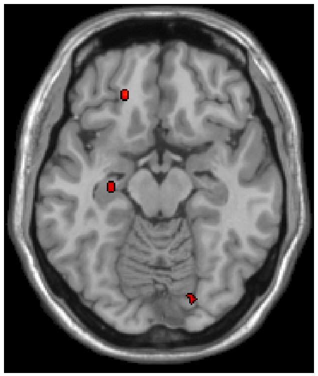
Sample images from the random effects analyses

The images on the following pages provide a sample of the activations observed in the random effects analyses. These are not the only sensory-motor areas active during the property verification task. Instead, images shown on each slide were representative of activity in sensory-motor regions while participants performed the property verification task. The top of each page provides the SPM99 contrast from which the image was taken (e.g., visual property verification minus the lexical decision condition). The Z coordinates located above each image provide the height (in MNI coordinates) of the slice that is shown. For contrasts in which a sensory-motor area was not active (e.g., auditory areas during motor property verification), a black square is shown.

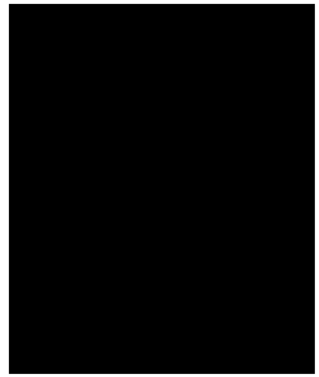
Visual property verification minus the lexical decision condition

Visual areas

Z = -14



Auditory areas

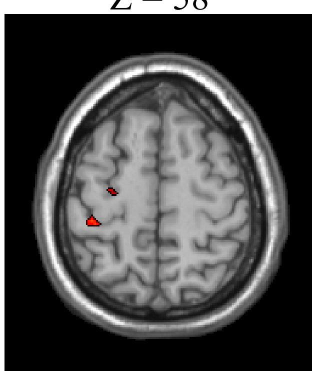


Motor areas

Z = 56

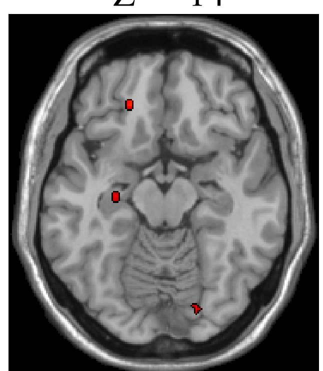
Somato- sensory areas

Z = 58



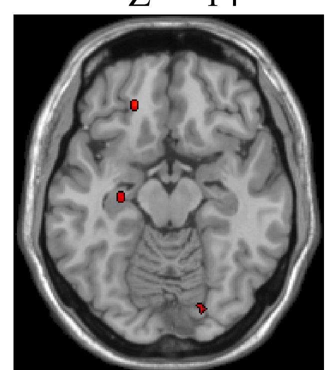
Gustatory areas

Z = -14



Olfactory areas

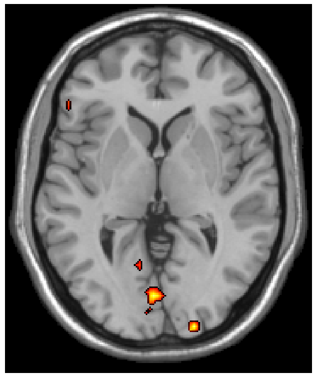
Z = -14



Auditory property verification minus the lexical decision condition

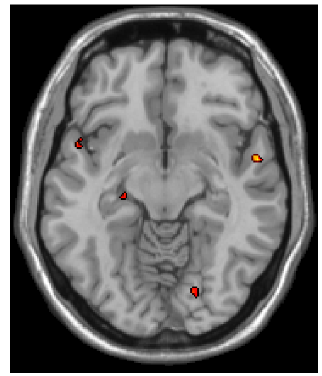
Visual areas

Z = 2



Auditory areas

Z = -10



Motor areas

Z = 72

Somato-sensory areas

Z = 64

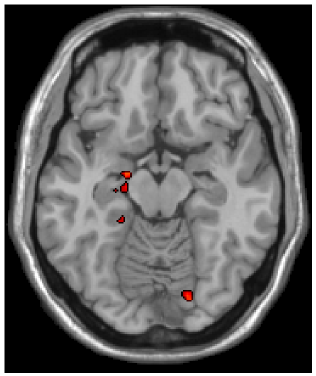
Gustatory areas

Olfactory areas

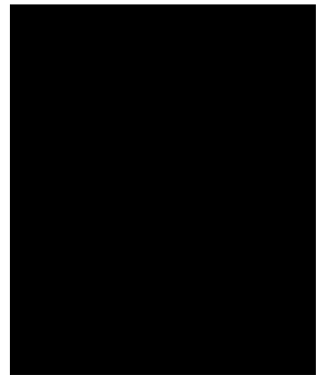
Motor property verification minus the lexical decision condition

Visual areas

Z = -14

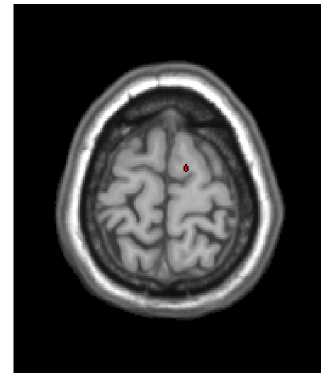


Auditory areas



Motor areas

Z = 70



Somato-sensory areas

Z = 76

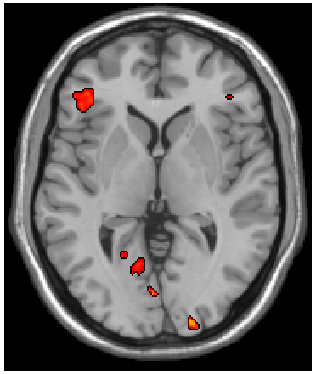
Gustatory areas

Olfactory areas

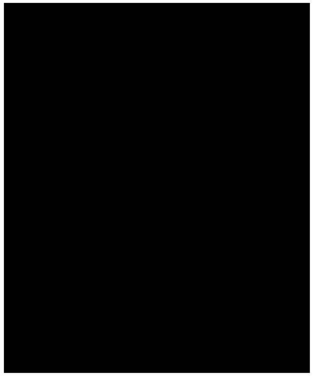
Somatosentory property verification minus the lexical decision condition

Visual areas

Z = 2



Auditory areas



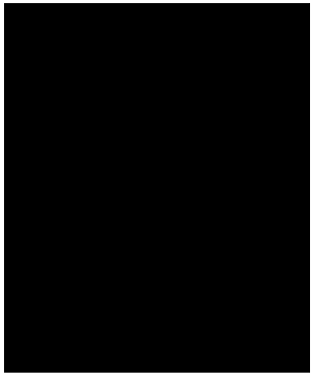
Motor areas

Z = 76

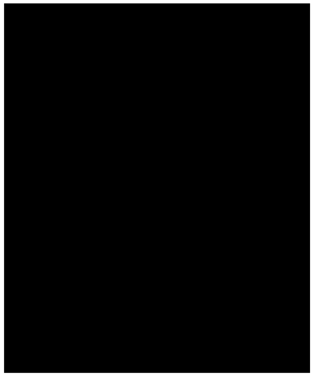
Somato-sensory areas

Z = 66

Gustatory areas



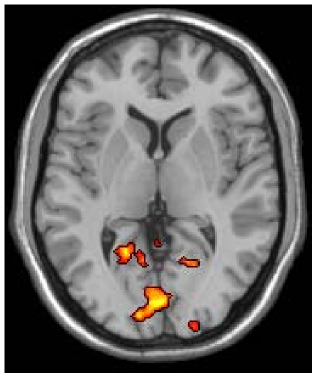
Olfactory areas



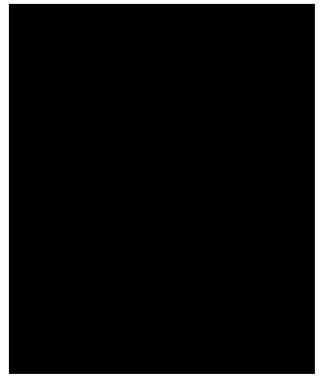
Gustatory property verification minus the lexical decision condition

Visual areas

Z = 4

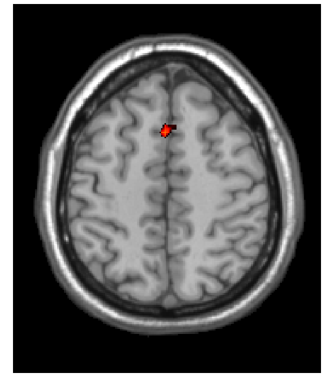


Auditory areas



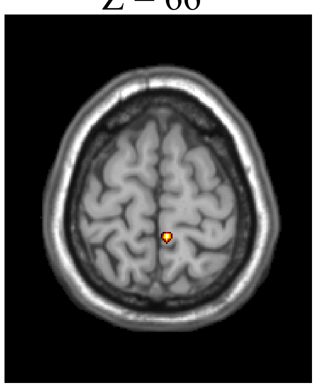
Motor areas

Z = 51



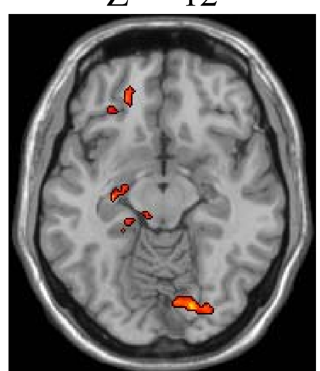
Somato-sensory areas

Z = 66



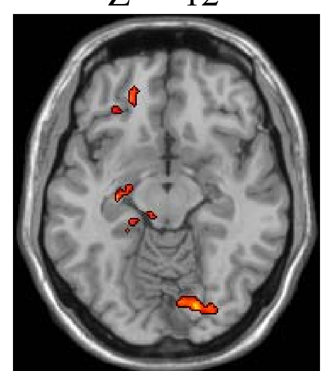
Gustatory areas

Z = -12



Olfactory areas

Z = -12



Olfactory property verification minus the lexical decision condition