Running Head: DECISION-MAKING AND LANGUAGE

Decision-making in the real world: A neuroeconomic framework for language processing

Corey T. McMillan1\*, Delani Gunawardena1, Robin Clark2 and Murray Grossman1

1University of Pennsylvania School of Medicine, Department of Neurology

2University of Pennsylvania, Department of Linguistics

\*Corresponding Author: University of Pennsylvania Medical Center

Department of Neurology

3400 Spruce Street, 3 West Gates

Philadelphia, PA 19104

mcmillac@mail.med.upenn.edu

Acknowledgments: This work was supported by the following grants from the National Institutes of Health: HD050406, NS44266, AG17586, AG15116, NS53488 and AG32953

Keywords: decision-making; language processing; homonyms; BOLD fMRI; lexical semantics

**Abstract**

**Introduction**

**Methods**

*Participants*

18 healthy young adults (11 female; mean age=25.3 years; mean education=15.1 years) from the University of Pennsylvania community participated in the study for monetary payment. All participants were native speakers of English, right-handed, and in good health with no history of neurological or psychiatric difficulty. Informed consent was obtained from all participants according to a protocol approved by the University of Pennsylvania Institutional Review Board. We excluded two participants from our analyses due to data corruption and therefore all results reported are for 16 participants.

*Experimental Materials*

We determined the preferred meanings of 50 noun-noun homonyms (e.g., “pen”) in a free association task in which 20 native English-speaking adults listed the first four words that came to mind. From this list we identified 20 homonyms which yielded 90% or more of total responses referring to one meaning (e.g., for “pen,” responses like “ink”, “pencil”, “paper”) and 10% or fewer total responses referring to another meaning (e.g., for “pen”, responses like “pig”, “sheep”, “farm”). We refer to the former as the *dominant* meaning and the latter as the *subordinate* meaning. We limited our selection of homonyms to 20 items because this subset of pretested homonyms contained a clear dominant and subordinate meaning and this number of items constitutes the minimum number needed to interpret data collected in an fMRI experiment with sufficient statistical power while minimizing the scan duration for the participant’s comfort.

We also generated 2 *context sentences* for each homonym (e.g., “Kim had some X”). As summarized in Table 1, the final word was semantically-related to the dominant meaning of the homonym in 20 context sentences (e.g., for PEN(writing instrument), “ink”); in another 20 context sentences, the final word was related to the subordinate meaning of the homonym (e.g., for PEN(animal cage), “pigs”). The semantic-relatedness of each biasing word relative to each homonym was evaluated on a 1 (unrelated) -7 (related) scale in a pretest completed by 20 different native English-speaking adults. This pretest revealed that the dominant-homonym pairs (e.g., ink-pen) were as semantically related as the subordinate-homonym pairs (e.g., pigs-pen; t(19)=1.39, p=0.2). The materials generated to create the dominant and subordinate context sentences thus are sufficiently semantically-related to bias the reader toward the intended meaning of the context for each homonym.

We also generated a semantically-neutral *carrier sentence* for each homonym that consisted of a simple phrase followed by a blank space (e.g., “She needed a \_\_\_\_\_.”). As indicated in Table 1, the same carrier sentence was used for both contexts (dominant, subordinate) of each homonym.

Lastly, we generated semantically-related *unambiguous alternatives* (e.g., “quill” and “cage”) for each meaning of each homonym (e.g., PEN). These were determined by presenting a cohort of 20 different native English-speaking adults each context sentence and carrier sentence containing the homonym (e.g., “Kim had some ink. She needed a pen”) and instructing them to replace each underlined word with a related word that maintains the same meaning of the sentence. We selected the most frequent response produced across participants that is not itself a homonym (e.g., “quill”). These responses did not differ statistically in lexical frequency (Francis et al., 1982) from the homonym in the dominant [t(19)=1.75, p=0.1] and subordinate contexts [t(19)=1.64, p=0.1].

Using these materials we generated a total of 40 experimental trials composed of 20 homonyms repeated in each of the two contexts (dominant, subordinate), as in Table 1. The same 20 homonyms were intentionally repeated in each context to minimize the possibility that differences observed across each context were due to the explicit context manipulation rather than due to potential differences in the choice of homonym in the experimental materials. In each experimental trial, participants were presented successively with a homonym and an unambiguous alternative, a context sentence, and a carrier sentence.

In order to obscure the repetition of each homonym across the experimental contexts we also generated an additional 200 filler trials that followed the same format as the experimental trials but did not include a homonym (e.g., “Tom loved breakfast. He ate a donut/bagel”). The large ratio of 1 experimental homonym trial to 5 filler trials was used in an attempt to limit the participants’ ability to simply perform a homonym detection task.

*Experimental Procedure*

We used a forced choice sentence completion paradigm. Participants were told that their task was to help us generate materials for a new experiment. They were further instructed “to be careful because some words like ‘pitcher’ can be ambiguous. An ambiguous word is a word that has more than one meaning”. They were given feedback for one trial and then performed another 8 practice trials without feedback.

For each experimental trial, participants were presented with three events; once each event was presented, it remained on the screen for the duration of the trial. This presentation method was used to minimize the amount of task-related executive resources that were required to perform the task (e.g., working memory to recall a previous event). As illustrated in Figure 1, the first event presented two written choices, one homonym (e.g., “pen”) and one unambiguous alternative (e.g., “quill”), in a counterbalanced placement on the left or right of the screen for 3000msec. In the second event, participants were presented with a written context sentence (e.g, “Kim had some ink”) for 3000msec. In the third event, participants were presented with the written carrier sentence (e.g, “She needed a \_\_\_\_.”) for 3000msec. Participants completed the sentence by responding with a left or right button press using a fiber-optic response pad to indicate the word they preferred to complete the carrier sentence. We report the proportion of unambiguous alternative responses.

Experimental and filler items were randomly distributed into 5 equal length runs with a duration of 9 minutes and counterbalanced so that each run contained the same proportion of each trial type and only included one presentation of each homonym. Within each trial, each event including the presentation of choices, context sentence, and completion sentence was presented synchronously with the onset of the MRI scanner TR (3000ms).

*MRI Acquisition & Analysis*

Scans were acquired on a Siemens 3.0T Trio scanner. Each session began with acquisition of a high-resolution T1-weighted structural volume using an MPRAGE protocol (TR = 1620 ms, TE = 3 ms, flip angle = 15°, 1 mm slice thickness, 192 × 256 matrix, resolution = .9766 × .9766 × 1 mm). A total of 955 BOLD fMRI images were acquired in 5 separate runs of equal length. Each image was acquired with fat saturation, 3 mm isotropic voxels, flip angle of 15°, TR = 3 s, TEeff = 30 ms, and a 64 × 64 matrix.

Image preprocessing and statistical analyses were performed using SPM5 (Wellcome Trust Centre for Functional Neuroimaging, London, UK). We first modeled each individual participant’s data. Low-frequency drifts were removed with high-pass filtering using a cutoff period of 128 s and autocorrelations were modeled using a first-order autoregressive model. Images for each participant were realigned to the first image in the series (Friston et al., 1995) and coregistered with the structural image (Ashburner and Friston, 1997). The transformation required to bring a participant’s images into standard MNI152 space was calculated using tissue probability maps (Ashburner & Friston, 1997), and these warping parameters were then applied to all functional images for that participant. During spatial normalization, functional data were interpolated to isotropic 2 mm voxels. The data were spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel.

For each stimulus category, hemodynamic response was estimated by convolving the onset times of the explicit decision event with a canonical hemodynamic response function. A general linear model approach was used to calculate parameter estimates for each variable for each subject, and linear contrasts for comparisons of interest. These estimates were then entered into second-level random effects analyses to allow us to make inferences across participants. In our initial analyses we report regions of activation relative to a resting baseline which survive a height threshold of t>5.96 (p<0.0001 uncorrected) and in the direct subtractions of closely matched materials we report regions of activation that survive a height threshold of t>4.01 (p<0.0005 uncorrected). In all comparisons we report clusters that contain a minimum of 20 adjacent voxels and have a peak voxel that exceeds a statistical cut-off criterion of p<0.05 (FDR-corrected).

**Results**

*Behavioral results*

To evaluate the relative roles of probability and risk in language we conducted a two-way ANOVA with Probability (Weak Preference, Strong Preference) and Risk (Less, More) as within-participant factors. We observed a significant main effect for probability [F(1,15)=10.20; p<0.01] in which participants selected single-meaning alternatives more often when the homonym had a weakly preferred meaning (M=0.77; SD=0.19) compared to a strongly preferred meaning (M=0.66; SD=.19). We did not observe a significant main effect for Risk [F(1,15)=1.53; p=0.24] or a Probability X Risk interaction [F(1,16)<1]. Refer to Figure 2.

The range of the participant’s rate of selecting unambiguous alternatives was very large as indicated by the high standard deviations. For example, the overall rate of selecting alternatives across all conditions ranged from 0.41 to 0.99. This observation suggests that there may be individual differences in a participant’s likelihood to choose an unambiguous alternative to a homonym in a subordinate context. To further investigate whether there are different patterns of performance on the task, we first calculated the chance rate of selecting one of two responses using a binomial test. This test revealed that selecting 14 (70%) or more alternatives out of 20 possible responses per condition differs significantly from chance (p<0.05). We then created two subgroups of participants using a criterion of a 70% alternative selection rate. This revealed that 10 participants significantly select alternatives to a homonym with a single associated meaning at a level that exceeds chance, and that 6 participants did not differentially prefer a single-meaning alternative to a homonym in the subordinate condition. We refer to these subgroups as “risk-averse” and “risk-neutral”, respectively.

Taking into account individual differences we conducted an ANOVA analysis, as above, with Probability (Weak Preference, Strong Preference) and Risk (Less, More) as within-participant factors and additionally included Group (Risk-Averse, Risk-Neutral) as a between participant factor. We observed a significant main effect of probability [F(1,14)=8,10; p=0.01], as above, a significant Risk X Group Interaction [F(1,14)=13.58; p<0.005] and all other main effects and interaction were not significant (all p>0.30). The risk-averse group selected single meaning alternatives more often in conditions of More Risk (M=0.91, SD=0.08) than conditions of Less Risk (M=0.77, SD=0.12) and this difference was significant [t(9)=3.85; p<0.005]. However, the risk-neutral group did not differentially select alternatives in the More Risk (M=0.49, SD=0.11) and Less Risk (M=0.59, SD=0.12) conditions [t(6)=2.18, p=0.07], though there was a trend towards the opposite pattern of the risk-averse group in which the risk-neutral participants selected alternatives more in Less Risk conditions than More Risk conditions. Overall, the risk-averse group selected alternatives more often that the risk-neutral group in both risk conditions: Less Risk [t(15)=2.97, p=0.01]; More Risk [t(15)=8.79, p=0.000]. Refer to Figure 3.A for risk-neutral group results and Figure 3.B for risk-averse group results.

Together, these results suggest that while all participants are sensitive to the probability of a homonym’s meaning, there are clear individual differences in participants’ sensitivity toward risk. Specifically, risk-averse participants select non-homonymous alternatives greater than chance and additionally select alternatives more often when there is more risk associated with selecting a homonym. It therefore appears that these participants are maximizing expected utility by taking into account the probability and risk associated with making a linguistic choice. However, the risk-neutral group are only sensitive to probability and do not consider the risk associated with making a linguistic choice. We use these subgroups identified by the behavioral data in the BOLD fMRI analyses below in order to determine the neural mechanisms that support decision-making in language.

*Neuroimaging Results*

To determine the neural mechanisms that support the hypothesized probabilistic evaluation component of making a linguistic decision we performed a parametric analysis of probability for the entire group of participants. This analysis revealed a parametric increase in activation in several regions associated with an increasing strength of preference for a homonym’s meaning. For example, “pen” has a strong preference for a particiular meaning (e.g., PEN(writing instrument)) while “bat” has a weak preference for a given meaning. Regions that revealed an increase in activation included bilateral DLPFC, left fusiform, left posterolateral temporal cortex, and the right thalamus. Refer to Table 2 for a summary of activated regions and Figure 4 for an illustration.

To determine the neural mechansism that support the hypothesized risk component of making a linguistic choice we evaluated activation during More Risk conditions relative to Less Risk conditions within each subgroup of participants (risk-averse, risk-neutral). We observed that risk-averse participants recruited ventromedial prefrontal

**General Discussion**

The current study investigated the neural mechanisms that support the process of using context to resolve a homonym’s meaning during sentence comprehension. A whole brain analysis demonstrated that, as a group, readers recruit neuroanatomic regions previously implicated in homonym comprehension, including posterolateral temporal and IFC. However, the behavioral results established evidence that there were individual differences in performance during the homonmym comprehension task. One group, which we call “strategizers,” completed sentences with single-meaning alternatives significantly more often than homophones across two linguistic contexts. We argue that this group appreciated both potential meanings of the homonym. Moreover, individuals in the strategizer subgroup upregulated DLPFC, OFC and parietal cortex to support the increased demands associated with homonym processing in the subordinate context compared to the dominant context. We associate these demands with strategic decision-making resources associated with interpreting a homonym’s meaning. We discuss the contribution of each of these regions below.

The observation of left posterolateral temporal activation is consistent with previous investigations of the comprehension of homonyms (Rodd et al., 2005b; Gennari et al., 2007) and sentences (Ni et al., 2000; Friederici et al., 2003; Humphries et al., 2006). According to one perspective, this region plays a key role in the interpretation of word meaning (Hickok and Poeppel, 2007). Another view argues that posterolateral temporal cortex is a multimodal integration area that contributes to the organization of conceptual information underlying lexical representations of concepts and propositions (Grossman et al., 2007). A third approach asserts that posterolateral temporal cortex is specifically implicated in lexical selection rather than conceptual processing per se (Indefrey and Levelt, 2004; Kemeny et al., 2006). Regardless of the specific role that posterolateral temporal cortex plays in lexical semantic processing, our observation of increased activation in this region in all contexts may be related to upregulation of a portion of the core language processing network that helps establish word meaning.

*Dorsolateral prefrontal cortex (DLPFC)*

We observed that DLPFC was parametrically recruited to support increased preference for a homonym’s meaning. DLPFC activation is perhaps most commonly reported in studies of strategic processing required to select among multiple alternative outcomes on decision-making tasks involving Stroop-like conflict (Cohen et al., 2000; MacDonald et al., 2000) and selecting a target from pairs of geometric shapes displaying many features (Badre and D'Esposito, 2007; Badre et al., 2009). Previous investigations evaluating probability have suggested that increased DLPFC activation on tasks such as these may be due in part to evaluating the probabilistic demands associated with a task (Casey et al., 2001; Huettel et al., 2005; Miller et al., 2005). Activation of DLPFC is rare in studies of language processing. In previous work assessing the processing of a temporary structural ambiguity in a sentence, DLPFC activation was seen during the evaluation of sentences where the main verb was embedded in a sentence structure with which it is less frequently associated compared to a sentence structure with which it is more frequently associated (Novais-Santos et al., 2007a). Our observation of increased DLPFC activation associated with the increasing probability of a homonym’s meaning is consistent with this account – the subordinate context requires individuals to evaluate a homonym for its less probable meaning, while in the dominant context participants have little need to access a less-probable meaning.

DLPFC activation also has been reported to support task difficulty and working memory (Braver et al., 1997; Cohen et al., 1997). However, we argue that such an account cannot fully explain our observation of selective recruitment of DLPFC. All materials were grammatically simple, short sentences consisting of familiar words, the stimuli were presented visually on the screen, and these stimuli were available throughout the duration of a trial in order to minimize working memory resources required for task performance. It is also unlikely that the subordinate context was simply “harder” than the dominant context in some non-specific sense since length and lexical frequency of materials were carefully matched across contexts. Additional work is needed to evaluate the precise contribution of DLPFC during language processing.

*Orbital frontal cortex (OFC)*

WE observed OFC activation and this activation was also greater in the subgroup of strategizers compared to non-strategizers. OFC activation is often associated with inhibitory control (Horn et al., 2003) and task-switching (Braver et al., 2003). Both experimental contexts involved inhibiting one of two forced-choice responses and we observed OFC activation in both contexts. It is unlikely that OFC is activated simply to inhibit activation of the dominant meaning of a homonym since OFC also was recruited in the dominant condition, albeit less so than in the subordinate condition. Likewise, both contexts may require switching between choices. Since we observed greater recruitment of OFC in the subordinate context, it is not clear how inhibitory control or task-switching accounts would fully explain this pattern of relatively greater OFC activation for a specific context.

An alternative interpretation of OFC activation is that this region has often been implicated as supporting the calculation of risk during decision-making (Bechara et al., 1994; Rolls, 2000; Breiter et al., 2001; Salmon et al., 2003; Fiddick et al., 2005), but this interpretation has rarely been applied to models of language processing. In a context consistent with a subordinate meaning, the interpretation of a homonym is risky since it has a higher likelihood of being misunderstood than when the homonym is embedded in a sentence context consistent with its dominant meaning. For example, there is a risk in a subordinate context that the use of the word PEN will be associated with its dominant meaning (writing instrument) rather than the intended but less frequently associated meaning (animal cage), while in a dominant context it is highly likely that PEN will be associated with its more frequent meaning (writing instrument). While some human and primate work associates OFC with a relative assessment of value (Tremblay and Schultz, 1999; Elliott et al., 2008), other studies suggest that OFC plays a particular role in the evaluation of a negative consequence following from a decision (O'Doherty et al., 2001; Yacubian et al., 2006; Wheeler and Fellows, 2008).

*Inferior parietal cortex*

Inferior parietal cortex was also activated in the comparison of the subordinate relative to the dominant context. Inferior parietal cortex has been reported in other homonym comprehension tasks (Bedny et al., 2008; Grindrod et al., 2008a; Hoenig and Scheef, 2009) and sentence comprehension tasks in general (Almor et al., 2007; Novais-Santos et al., 2007b). However, the contribution of inferior parietal cortex for language processing is not well understood. Others have proposed that it supports the inhibition of a semantic meaning (Hoenig and Scheef, 2009), it is upregulated to support increased working memory demands associated with resolving ambiguity (Novais-Santos et al., 2007b), or that it integrates multiple sources of linguistic information (Almor et al., 2007). In the following section we propose a novel account for inferior parietal cortex as a component of a large-scale network that supports homonym comprehension.

*A fronto-parietal network*

Together, DLPFC, OFC, and inferior parietal cortex contribute to the resolution of a homonym’s meaning. Studies on decision-making have implicated these regions as contributing to a large-scale network that supports the calculation of expected utility when making a decision. Expected utility (EU) is generally defined as the probability of an event (P) times the value of an outcome (V), where value is equal to cost (C) minus risk (R), or EU = P \* (C - R). A recent linguistic model proposed that individuals use expected utility to make linguistic choices that maximize communicative clarity (Clark and Parikh, 2007; Clark, in press). According to this account, “probability” would refer to the likelihood of a homonym meaning in a specific context and would be supported by a probabilistic neural mechanism such as DLPFC. “Value” would refer to the difference between the working memory and attentional resource “costs” required to evaluate an alternative word (e.g., considering an alternative meaning of “pen” in a dominant context may not be worthwhile) and would be supported by value mechanism such as OFC. Lastly, expected utility would require the integration of probabilistic information about a homonym’s meaning and value information and would be supported by a neural mechanism known to contribute to integration. Previous neuroimaging studies have demonstrated that inferior parietal cortex contributes to integrating the probability and risk components of a decision into a single currency such as expected, or physiological, utility (Platt and Glimcher, 1999; Paulus et al., 2001; Huettel et al., 2005).

The observation that there are individual differences in the performance of two subgroups of participants requires some additional investigation to determine why some individuals interpret homonyms differently than other individuals. Individuals who decided to complete a sentence with a non-homonymous word also showed greater recruitment of a frontal-parietal decision-making network in a subordinate context compared to a dominant context. One potential account for these different behavioral performance patterns is that it has long been established that individuals widely vary along a continuum of risk-aversive and risk-taking behavior. In the context of our proposed decision-making model, it is possible that strategizers are relatively risk averse and therefore complete sentences so they are more likely to be understood. Other potential accounts include the possibilities that strategizers had increased word knowledge of the homonyms and therefore were more likely to appreciate the subordinate meaning, or that the strategizers had greater working memory resources and were therefore more able to select an alternative. It is unfortunate that we did not assess these characteristics in the individuals participating in the present study, and an important direction for future empirical enquiry will evaluate how individual differences in risky behavior, word knowledge, and working memory account for some individual differences in lexical processing. Additionally, it is necessary to evaluate why the non-strategizers did not differentiate between homonyms and alternatives or between sentence contexts. By accounting for individual differences such as these, researchers may be able to resolve conflicting psycholinguistic findings, such as those demonstrating that individuals do strategically use communication (Haywood et al., 2005) and those that do not (Ferreira, 2008).

A potential limitation of the current study is concerned with the relatively small number of stimuli involving selection of a homonym or a unique alternative in each context. The neuroanatomic regions recruited during the selection of a homonym response may differ from those regions recruited when participants selected an unambiguous alternative response, and this may have confounded our assessment of strategic decision-making in language. For example, it has been demonstrated that activation of brain regions associated with making a financial decision in a non-linguistic “shopping” task can be used to predict a participant’s response (Knutson et al., 2007). We were unable to perform a similar analysis in the current study because the limited statistical power associated with the outcome of such an analysis in our dataset would render the results difficult to interpret. The small number of stimuli also prevented us from determining the extent to which participants “activated” the dominant or subordinate meaning of each homonym. Finally, the limited amount of available time for collecting additional data prevented us from determining the component of the decision-making model that has the greatest impact on the activation pattern, namely, maximizing the likelihood of being understood, minimizing the risk associated with misinterpretation, or both. Future research that evaluates the different neural responses associated with a specific linguistic choice with a larger sampling of stimuli will allow us to have enough data to help constrain our proposed model of strategic decision-making for language in a more informed manner.

With these caveats in mind, we found that a subset of individuals strategically completed sentences with non-homonymous words that were otherwise likely to be misinterpreted. Furthermore, we demonstrated that the neural basis for this process does not appear to depend exclusively on an automatic mechanism that resolves semantic competition in IFC. Instead, our observations are consistent with an account that proposes that proposes strategic decision-making resources situated in a frontal-parietal network contribute to using context in order to resolve a homonym’s meaning. These findings highlight the importance for integrating strategic decision-making resources into models of language processing.

References

Almor A, Smith DV, Bonilha L, Fridriksson J, Rorden C (2007) What is in a name? Spatial brain circuits are used to track discourse references. In: Neuroreport, pp 1215-1219.

Ashburner J, Friston K (1997) Multimodal image coregistration and partitioning--a unified framework. Neuroimage 6:209-217.

Badre D, Wagner A (2002) Semantic retrieval, mnemonic control, and prefrontal cortex. In: Behav Cogn Neurosci Rev, pp 206-218.

Badre D, D'Esposito M (2007) Functional magnetic resonance imaging evidence for a hierarchical organization of the prefrontal cortex. J Cogn Neurosci 19:2082-2099.

Badre D, Hoffman J, Cooney JW, D'Esposito M (2009) Hierarchical cognitive control deficits following damage to the human frontal lobe. Nat Neurosci 12:515-522.

Badre D, Poldrack RA, Pare-Blagoev EJ, Insler RZ, Wagner AD (2005) Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. Neuron 47:907-918.

Bechara A, Damasio AR, Damasio H, Anderson SW (1994) Insensitivity to Future Consequences Following Damage to Human Prefrontal Cortex. Cognition 50:7--15.

Bedny M, McGill M, Thompson-Schill SL (2008) Semantic adaptation and competition during word comprehension. In: Cereb Cortex, pp 2574-2585.

Bilenko NY, Grindrod CM, Myers EB, Blumstein SE (2009) Neural correlates of semantic competition during processing of ambiguous words. J Cogn Neurosci 21:960-975.

Botvinick M, Nystrom LE, Fissell K, Carter CS, Cohen JD (1999) Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402:179-181.

Braver TS, Reynolds JR, Donaldson DI (2003) Neural mechanisms of transient and sustained cognitive control during task switching. Neuron 39:713-726.

Breiter HC, Aharon I, Kahneman D, Dale A, Shizgal P (2001) Functional Imaging of Neural Responses to Expectancy and Experience of Monetary Gains and Losses. Neuron 30:619--639.

Brett M, Anton J-L, Valabregue R, Poline J-B (2002) Region of interest analysis using an SPM toolbox. In: 8th International Conference on Functional Mapping of the Human Brain. Sendai, Japan.

Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD (2000) Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. Proc Natl Acad Sci U S A 97:1944-1948.

Casey BJ, Forman SD, Franzen P, Berkowitz A, Braver TS, Nystrom LE, Thomas KM, Noll DC (2001) Sensitivity of prefrontal cortex to changes in target probability: a functional MRI study. Hum Brain Mapp 13:26-33.

Clark R (in press) Meaningful Games: Exploring Language with Game Theory. Cambridge, MA: MIT Press.

Clark R, Parikh P (2007) Game theory and discourse anaphora. In: Journal of Logic, Language and Information, pp 265-282.

Cohen JD, Botvinick M, Carter CS (2000) Anterior cingulate and prefrontal cortex: who's in control? Nat Neurosci 3:421-423.

Elliott R, Agnew Z, Deakin JF (2008) Medial orbitofrontal cortex codes relative rather than absolute value of financial rewards in humans. Eur J Neurosci 27:2213-2218.

Ferreira VS (2008) Ambiguity, Accessibility, and a Division of Labor for Communicative Success. In: The Psychology of Learning and Motivation: Advances in Research and Theory (Benjamin AS, Ross BH, eds), pp 209--246. London: Academic Press.

Fiddick L, Spampinato MV, Grafman JH (2005) Social contracts and precautions activate different neurological systems: An fMRI investigation of deontic reasoning. NeuroImage 28:778-786.

Francis WN, Kucera H, Mackie AW (1982) Frequency analysis of English usage : lexicon and grammar. Boston: Houghton Mifflin.

Friederici AD, Ruschemeyer SA, Hahne A, Fiebach CJ (2003) The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. Cereb Cortex 13:170-177.

Friston KJ, Ashburner J, Frith CD, Poline J-B, Heather JD, Frackowiak RSJ (1995) Spatial registration and normalization of images. Human Brain Mapping 3:165-189.

Gennari SP, MacDonald MC, Postle BR, Seidenberg MS (2007) Context-dependent interpretation of words: evidence for interactive neural processes. Neuroimage 35:1278-1286.

Grindrod C, Bilenko N, Myers E, Blumstein S (2008a) The role of the left inferior frontal gyrus in implicit semantic competition and selection: An event-related fMRI study. In: Brain research, pp 167-178.

Grindrod CM, Bilenko NY, Myers EB, Blumstein SE (2008b) The role of the left inferior frontal gyrus in implicit semantic competition and selection: An event-related fMRI study. Brain Res 1229:167-178.

Grossman M, Troiani V, Koenig P, Work M, Moore P (2007) How necessary are the stripes of a tiger? Diagnostic and characteristic features in an fMRI study of word meaning. Neuropsychologia 45:1055-1064.

Haywood SL, Pickering MJ, Branigan HP (2005) Do speakers avoid ambiguities during dialogue? Psychological Science 16:362-366.

Hickok G, Poeppel D (2007) The cortical organization of speech processing. Nat Rev Neurosci 8:393-402.

Hillis AE, Wityk RJ, Tuffiash E, Beauchamp NJ, Jacobs MA, Barker PB, Selnes OA (2001) Hypoperfusion of Wernicke's area predicts severity of semantic deficit in acute stroke. Ann Neurol 50:561-566.

Hoenig K, Scheef L (2009) Neural correlates of semantic ambiguity processing during context verification. In: NeuroImage, pp 1009-1019.

Horn NR, Dolan M, Elliott R, Deakin JF, Woodruff PW (2003) Response inhibition and impulsivity: an fMRI study. Neuropsychologia 41:1959-1966.

Huettel SA, Song AW, McCarthy G (2005) Decisions under Uncertainty: Probabilistic Context Influences Activation of Prefrontal and Parietal Cortices. J Neurosci 25:3304-3311.

Humphries C, Binder JR, Medler DA, Liebenthal E (2006) Syntactic and semantic modulation of neural activity during auditory sentence comprehension. J Cogn Neurosci 18:665-679.

Indefrey P, Levelt WJM (2004) The Spatial and Temporal Signatures of Word Production Components. Cognition 92:101-144.

Kemeny S, Xu J, Park GH, Hosey LA, Wettig CM, Braun AR (2006) Temporal dissociation of early lexical access and articulation using a delayed naming task--an FMRI study. Cereb Cortex 16:587-595.

Knutson B, Rick S, Wimmer GE, Prelec D, Loewenstein G (2007) Neural predictors of purchases. Neuron 53:147-156.

MacDonald AW, 3rd, Cohen JD, Stenger VA, Carter CS (2000) Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 288:1835-1838.

Mason RA, Just MA (2007) Lexical ambiguity in sentence comprehension. In: Brain Research, pp 115-127.

Miller MB, Valsangkar-Smyth M, Newman S, Dumont H, Wolford G (2005) Brain activations associated with probability matching. Neuropsychologia 43:1598-1608.

Ni W, Constable RT, Mencl WE, Pugh KR, Fulbright RK, Shaywitz SE, Shaywitz BA, Gore JC, Shankweiler D (2000) An event-related neuroimaging study distinguishing form and content in sentence processing. J Cogn Neurosci 12:120-133.

Novais-Santos S, Gee J, Shah M, Troiani V, Work M, Grossman M (2007a) Resolving sentence ambiguity with planning and working memory resources: Evidence from fMRI. Neuroimage 37:361-378.

Novais-Santos S, Gee J, Shah M, Troiani V, Work M, Grossman M (2007b) Resolving sentence ambiguity with planning and working memory resources: Evidence from fMRI. In: NeuroImage, pp 361-378.

O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C (2001) Abstract reward and punishment representations in the human orbitofrontal cortex. Nat Neurosci 4:95-102.

Paulus MP, Hozack N, Zauscher B, McDowell JE, Frank L, Brown GG, Braff DL (2001) Prefrontal, parietal, and temporal cortex networks underlie decision-making in the presence of uncertainty. NeuroImage 13:91-100.

Platt ML, Glimcher PW (1999) Neural correlates of decision variables in parietal cortex. Nature 400:233-238.

Rodd J, Davis M, Johnsrude I (2005a) The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. In: Cerebral Cortex, p 1261.

Rodd JM, Davis MH, Johnsrude IS (2005b) The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. Cereb Cortex 15:1261-1269.

Rolls ET (2000) The orbitofrontal cortex and reward. Cerebral Cortex 10:284-294.

Salmon E, Garraux G, Delbeuck X, Collette F, Kalbe E, Zuendorf G, Perani D, Fazio F, Herholz K (2003) Predominant Ventromedial Frontopolar Metabolic Impairment in Frontotemporal Dementia. Neuroimage 20:435--440.

Thompson-Schill S, D'Esposito M, Aguirre G, Farah M (1997a) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. In: Proc Natl Acad Sci U S A, pp 14792-14797.

Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ (1997b) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc Natl Acad Sci U S A 94:14792-14797.

Tremblay L, Schultz W (1999) Relative reward preference in primate orbitofrontal cortex. Nature 398:704-708.

Wagner AD, Pare-Blagoev EJ, Clark J, Poldrack RA (2001) Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. Neuron 31:329-338.

Warrington EK, Shallice T (1984) Category specific semantic impairments. Brain 107 ( Pt 3):829-854.

Wheeler EZ, Fellows LK (2008) The human ventromedial frontal lobe is critical for learning from negative feedback. Brain 131:1323-1331.

Whitney C, Grossman M, Kircher TTJ (2009) The Influence of Multiple Primes on Bottom-Up and Top-Down Regulation during Meaning Retrieval: Evidence for 2 Distinct Neural Networks. In: Cerebral Cortex, pp 2548-2560.

Yacubian J, Glascher J, Schroeder K, Sommer T, Braus DF, Buchel C (2006) Dissociable systems for gain- and loss-related value predictions and errors of prediction in the human brain. J Neurosci 26:9530-9537.

Zempleni M, Renken R, Hoeks J, Hoogduin J, Stowe L (2007a) Semantic ambiguity processing in sentence context: Evidence from event-related fMRI. In: NeuroImage, pp 1270-1279.

Zempleni MZ, Renken R, Hoeks JC, Hoogduin JM, Stowe LA (2007b) Semantic ambiguity processing in sentence context: Evidence from event-related fMRI. Neuroimage 34:1270-1279.

Table 1

Example stimulus materials for the homonym “pen” in the Dominant and the Subordinate contexts

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Condition** | | **Sample Stimuli** | | **Sample Choices** | |
| **Probability** | **Risk** | **Context** | **Completion** | **Homonym** | **Alternative** |
| More Preferred | Less | Kim had some ink. | She needed a \_\_\_\_. | pen | quill |
| More Preferred | More |  |  |  |  |
| Less Preferred | Less | Kim had some pigs. | She needed a \_\_\_\_. | pen | cage |
| Less Preferred | More |  |  |  |  |

Neuroanatomic regions of activation and MNI coordinates for parametrically increasing activation associated with increasing probability of a homonym’s meaning.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Neuroanatomic Region (BA)** | **L/R** | **MNI Coordinates** | | | **Voxels** | **Z-score** |
| **Parametric Increase for Probability** | | | | | | |
| Dorsolateral prefrontal (46/9), inferior frontal (44) | L | -52 | 18 | 16 | 1462 | 5.00 |
| Dorsolateral prefrontal (46) | R | 52 | 36 | 6 | 270 | 4.20 |
| Fusiform (36), posterolateral temporal (37) | L | -48 | -48 | -18 | 325 | 4.14 |
| Thalamus, caudate tail | R | 34 | -40 | 10 | 231 | 4.11 |
| **More Risk > Less Risk for Risk-Averse Subgroup** | | | | | | |
| Thalamus | L | -18 | -14 | -6 | 8007 | 4.40 |
| Inferior parietal (39/40) | L | -58 | -58 | 26 | 471 | 4.12 |
| Inferior parietal (39/40) | R | 60 | -56 | 22 | 965 | 4.03 |
| Ventromedial prefrontal (10) | R | 14 | 56 | 4 | 439 | 3.66 |
| Dorsomedial prefrontal (9) | -- | -8 | 54 | 12 | 1146 | 3.61 |
| Thalamus | R | 22 | -16 | -6 | 278 | 3.42 |
| **Risk-Averse Subgroup > Risk-Neutral Subgroup for More Risk > Less Risk Contrast** | | | | | | |
| Insula (13) | R | 42 | -40 | 24 | 302 | 3.66 |
| Thalamus | L | -14 | -18 | 8 | 153 | 3.37 |
| Middle occipital (18) | L | -10 | -84 | 2 | 90 | 3.33 |
| Orbital frontal (10) | L | -40 | 48 | 0 | 95 | 3.29 |

Figure 1

An illustration of a typical experimental trial: Event 1 we presented two choices (a homonym and unambiguous alternative), Event 2 we presented a context sentence, Event 3 we presented a carrier sentence.

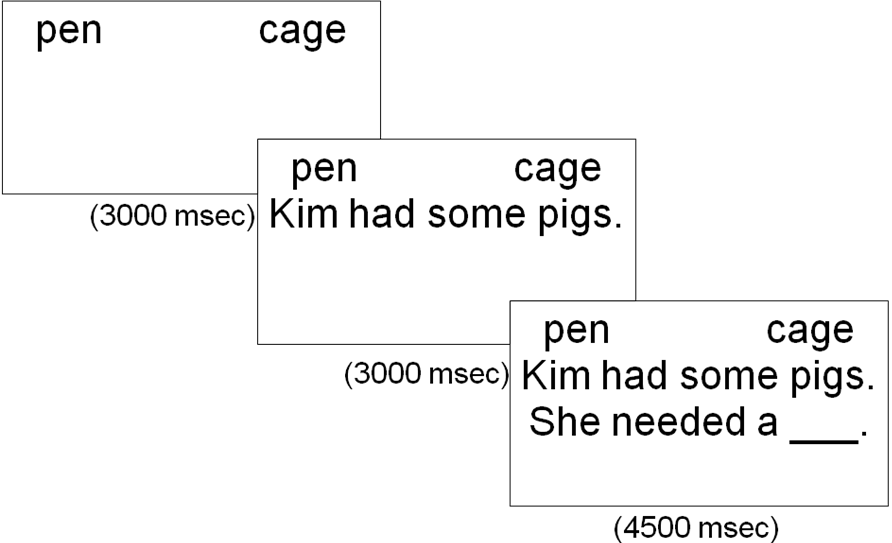
Figure 2. Mean proportion of non-homonym alternative choices

Table 3

Figure 3. Mean proportion of non-homonym alternative choices for (a) Risk-Neutral participants (N=6) and (b) Risk-Averse participants (N=10).

|  |  |  |
| --- | --- | --- |
| **a** |  |  |
| **b** |  |  |

Figure 4. Regions of BOLD activation which increased parametrically with increasing probability of a homonym’s meaning,

Probability_Lateral.tiff

Figure 5. Regions of BOLD activation for the contrast of More Risk minus Less Risk: (a) Risk-Averse group; (b) Risk-Averse > Risk-Neutral group

|  |  |
| --- | --- |
| **a** | AverseGroup_LateralandSlices.tiff |
| **b** | Averse-Neutralgroups.tiff |