How the brain learns how few are "many": An fMRI study of the flexibility of quantifier semantics

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Abstract

Previous work has shown that the meaning of a quantifier such as "many" or "few" depends in part on quantity. However, the meaning of a quantifier may vary depending on the context, e.g. in the case of common entities such as "many ants" (perhaps several thousands) compared to endangered species such as "many pandas" (perhaps a dozen). In a recent study (Heim et al. 2015 Front. Psychol.) we demonstrated that the relative meaning of "many" and "few" may be changed experimentally. In a truth value judgment task, displays with 40% of circles in a named color initially had a low probability of being labeled "many". After a training phase, the likelihood of acceptance 40% as "many" increased. Moreover, the semantic learning effect also generalized to the related quantifier "few" which had not been mentioned in the training phase. Thus, fewer 40% arrays were considered "few." In the present study, we tested the hypothesis that this semantic adaptation effect was supported by cytoarchitectonic Brodmann area (BA) 45 in Broca's region which may contribute to semantic evaluation in the context of language and quantification. In an event-related fMRI study, 17 healthy volunteers performed the same paradigm as in the previous behavioral study. We found a relative signal increase when comparing the critical, trained proportion to untrained proportions. This specific effect was found in left BA 45 for the trained quantifier "many", and in left BA 44 for both quantifiers, reflecting the semantic adjustment for the untrained but related quantifier "few." These findings demonstrate the neural basis for processing the flexible meaning of a quantifier, and illustrate the neuroanatomical structures that

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contribute to variable meanings that can be associated with a word when used in different contexts.

1. Introduction

"I don't know half of you half as well as I should like; and I like less than half of you half as well as you deserve" – with this remarkable phrase, Bilbo Baggins baffles his audience (Tolkien, 2007, p. 30). It is a fine example of how our brains are able to express complex numerical or proportional relations between sets, in this case the set of the entire audience, the proportion of the audience that Bilbo knows, and within the latter the ones he likes to various degrees. The words that we have in natural language to express these numerical or proportional relationships are called quantifiers – expressions like "less than half", "many", or "some". Quantifiers thus serve as a means to assign a truth value to a flexible representation of a concept that depends in part on number knowledge (Clark & Grossman, 2007). In this study, we examine more carefully the neuroanatomic basis for the flexible representation of the meaning of words like quantifiers.

The brain basis for quantifier processing has attracted an increasing amount of research. McMillan et al. (2005) compared BOLD amplitude differences related to systematically varying cognitive demands associated with different types of quantifiers. Whereas some quantifiers such as "at least seven" only require comparison of the actual number of objects to the explicitly given criterion "seven", the situation is more complex for an expression like "more than half". In the latter case, at least two steps are necessary instead of one: First, one has to assess what "half" of the given number of tokens is. This quantity must be kept in mind so that a comparison of the actual number of tokens to this value can be made. McMillan et al. found robust left and right inferior frontal activation differences between these first-order vs. higher-order quantifiers. Based on the available literature, they interpreted the observed difference as indication of increasing demands on the working memory system in higher-order quantifier processing. In addition, when comparing numerical quantifiers (e.g. "at least X") to Aristotelian quantifiers (e.g. "some"), Troiani et al. (2009) observed a functional link between (right) dorsolateral prefrontal cortex and the right intraparietal sulcus, thus linking the working memory network to that of abstract number representation. Also, studies of non-aphasic patients with impaired number knowledge show difficulty with quantifier comprehension have provided converging sources of evidence that suggest that not only do these areas activate to support quantifier comprehension, but are necessary in order to appreciate quantifier meaning (e.g. Troiani et al. 2011; Morgan et al. 2011; McMillan et al. 2006) or meaning in general.

Evidence for the importance of left Brodmann area (BA) 45 for processing of quantifier semantics came from a study by McMillan and colleagues (2013) who examined both the BOLD response in healthy adults and gray matter (GM) atrophy in patients with focal neurodegenerative disorders. Both groups of subjects had to process sentences in which quantifier meaning was ambiguous (thus posing higher semantic processing demands on the subjects) or unambiguous. Converging results from BOLD fMRI and brain atrophy pointed at the crucial role of left BA 45 for the successful access to quantifier meaning. As Wei et al.

(2012) have shown, BA 45 is also engaged in processing quantifiers in a completely different language like Chinese.

Heim et al. (2012) shed further light on the functional characterization of the frontal and parietal components of the quantifier processing network using a bi-parametric approach. Modelling actual proportion of target items and decision difficulty as independent regressors in the model, they were able to dissociate processes of initial estimation of numerosity from those of the comparison of that numerosity to an explicit (as in the case of numerical quantifiers) or implicit criterion (as in the case of e.g. "many", "some", or "few"). In particular in the left hemisphere, estimation and comparison recruited neighboring but largely non-overlapping regions in the inferior frontal and inferior parietal cortex. Most importantly, quantifier polarity (i.e. whether the quantifier has a positive notion as in "many" or "most" vs. a negative notion as in "few" or "less than X") as an index of the semantic content was related to left BA 45 in the left inferior frontal gyrus. Thus, three systems for estimation, comparison, and semantics could be identified in the left inferior frontal cortex, suggesting a particular role for that region for understanding quantifier expressions in natural language.

A critical attribute of quantifier meaning is its flexibility. Unlike a specific numerosity like "4," quantifier meaning is not fixed, and its meaning often depends on the context in which the quantifier is used. In the context of endangered species, "many" might denote five pandas. In the context of germs, by comparison, "many" would imply billions of microbes. Conversely, the numbers assigned to the quantifiers "very few", "few", "only a few", "a few", or "not many" were largely in the same range, thus allowing no semantic differentiation between these quantifiers (Moxey & Sanford, 1993; see also Moxey & Sanford, 2000) (see also Shikhare et al. 2015). Subjects thus tend to assign rank-ordered scopes to different quantifiers (Oaksford et al., 2002), where "few" denotes more than "none", for example, "many" more than "few", and "all" more than "many." However, there may be considerable flexibility in the assignment of meaning within each of these quantifiers.

We examined this flexibility of quantifier meaning experimentally in a recent behavioral experiment studying the quantifiers "many" and "few" (Heim et al., 2015). The experiments consisted of three blocks each. In a first baseline block, the investigators assessed the likelihood that a given number of yellow circles out of a total array of 50 blue and yellow circles would be called "many" or "few". In block 2, subjects received feedback for their button press responses. Using this feedback, we managed to shift the subjects' internal criterion for "many" from originally ~60% down to 40% of yellow circles. This shift persisted in the third block which was identical to block 1. Importantly, the criterion shift for the quantifier "many" also had an impact on the semantic judgments of the related quantifier "few." If 40% of circles were "many", then it was no longer possible for 40% of yellow circles to be considered "few," as had been the case during the baseline judgments in Block 1. Accordingly, the probability to call 40% "few" decreased in Block 3, even though an adjustment of the criterion for "few" had not been mentioned. In sum, we observed a shift in the criterion that was not restricted to one explicitly manipulated quantifier but that generalized to the complementary quantifier as well. A second experiment confirmed that

this mechanism also worked in the other direction, with explicit training for "few" and implicit transfer to "many".

We used this paradigm to further investigate the neuroanatomical basis for the mental flexibility of quantifier meaning. More broadly, this paradigm may also provide insight into how the brain can adaptively compute meaning. Based on the neurocognitive literature referred to above, we hypothesized that left inferior frontal cortex, and in particular its BA 45, is essential for the semantic (re-)evaluation of flexible quantifier meaning. Accordingly, we administered an almost identical version of the original paradigm inside the scanner, only adding null events for reasons of model optimization, to examine the neuroanatomic basis for quantifier meaning.

2. Methods

2.1 Participants

Seventeen healthy right-handed, native English-speaking volunteers (mean age 22.3 years, range 19–29 years; 8 women; average amount of education: 15.9 years) participated in this study. Participants were recruited at the University of Pennsylvania, participated in an informed consent procedure approved by an Institutional Review Board convened at the University of Pennsylvania, and received $35 for their participation.

2.2 Procedure

Before entering the scanner, subjects were briefly familiarized with the stimuli and the upcoming task. Inside the scanner, subjects were presented with pictures showing isoluminant blue and yellow circles on a grey background. The stimuli were taken from the study by Heim et al. (2012). Each stimulus item was composed of 50 circles, of which a defined proportion of 20/30/40/50/60/70% was yellow while the other circles were blue. There were six different stimuli for each proportion (for more details cf. Heim et al., 2015).

Each picture was presented together with a written sentence, either "*Many* of the circles are yellow" or "*Few* of the circles are yellow". The subjects then performed a truth value judgment task, indicating whether or not they found this sentence correctly described the picture by pressing the left or right response button. The assignment of the YES/NO decisions to the response buttons was kept constant for each single subject for the duration of the experiment. Across subjects, the assignment was balanced such that eight of the subjects pressed the left button for YES and the right for NO and vice versa for the other nine subjects.

The experiment consisted of three blocks. In block 1, the baseline block, the subjects' internal criteria for "*many*" and for "*few*" were assessed. In block 2, the adaptation block, subjects received feedback for their responses. In this block, we provided feedback and only stimuli with the quantifier "*many*" were presented. Positive feedback was given if they responded YES to pictures containing 40% or more of yellow circles, or NO to pictures with less than 40% of yellow circles. Negative feedback was given if they responded NO to pictures with 40% or more yellow circles, or YES to less than 40% yellow circles. Based on previous data (Heim et al., 2015), this feedback was known to shift the internal criterion

from a presumed baseline of 50–60% down to 40%. The adaptation block consisted of 162 trials including 27 null events. Finally, block 3 was administered, which was identical to the baseline block. It served as a test block to assess in what way the internal criterion for *"many"* had been changed during the explicit training block for *"many"*, and how the criterion for *"few"* had been altered in parallel, even though *"few"* had never been presented in the adaptation block. The baseline and testing blocks included 18 null events each.

Each trial in the baseline and the test block was as follows. First, a written sentence (e.g. "Many of the circles are yellow") was shown in the upper third of the screen for 3,000ms. The sentence remained available for an additional 1,500ms while the stimulus array containing yellow and blue circles appeared at the center of the screen for the same amount of time. The words "YES" and "NO" were written in the lower third of the screen to indicate which button to press. Finally, the screen went blank for another 1,500ms before the next trial began.

The trials in the adaptation phase (block 2) were similar to those in the baseline/test phase, with the exception that feedback was given in these trials. If the subjects responded correctly, they gained 10 points which were added to their total score. False responses were penalized by subtracting 10 points from their score. The visual feedback consisted either of a green arrow pointing upward and the information "+ 10" in green print, or a downward red arrow and the text "− 10" in red. They all started with an initial score of "+ 100". The actual score was always presented in the center of the top part of the screen in black.

2.3 Acquisition of MRI data

Functional scans were acquired on a Siemens 3T Tim Trio scanner at the University of Pennsylvania Hospital. After a localizer scan, volumes were acquired in three runs, one for each experimental block (runs 1 and 3: 248 volumes each; run 2: 365 volumes). The BOLD contrast was measured with an echo-planar imaging sequence (TR = 3,000ms; TE = 30ms; flip angle 90°; matrix 64×64; FOV = 126; interleaved slices; resolution=3mm isotropic).

Finally, a structural T1-weighted scan was run using an MPRAGE sequence (TR = 1,620ms; TE = 3.09ms; flip angle = 15°; matrix 192×256; slice thickness = 1mm; in-plane resolution = 0.9×0.9 mm n slices = 160; sequential slices).

2.4 Analysis of behavioral data

The acceptability ratings were aggregated per subject, experimental block, quantifier, and proportion of circles of the target color. A $2 \times 2 \times 6$ ANOVA with factors QUANTIFIER (many/few), BLOCK (baseline/test), and PROPORTION (20/30/40/50/60/70) was run to test for differential learning effects for the trained quantifier MANY vs. the untrained quantifier FEW at trained (40%) vs. untrained proportions. Next, the 3-way interactions were investigated by running a 2×6 ANOVA with factors QUANTIFIER and BLOCK only for the critical proportion "40%". Finally, paired t-tests compared the change in acceptability ratings at the critical proportion "40%" for the trained and the untrained quantifier. We used one-tailed t-tests because of our a priori predictions.

2.5 Analysis of fMRI data

The fMRI data were analyzed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/) running on Matlab 7.8 (The Mathworks Inc.). Preprocessing of individual data sets included the standard procedures of realignment to the first slice (separately for each of the three runs), normalization into the standard MNI reference space, and spatial smoothing with a Gaussian kernel of 8mm FWHM. Next, the hemodynamic response was modelled separately for each condition in an event-related fixed-effects design at the first level. To this end, for each subject, the onset vectors for those trials of each condition considered for the analysis of the behavioral data were convolved with the canonical HRF and its first time derivative, using the duration of the actual presentation of the stimulus image (3,000ms) as duration parameter. The standard high-pass filter of 1/128Hz was used to eliminate slow physiological drifts from the signal. For each subject, each condition regressor was then contrasted against the resting baseline, i.e. the null events, to obtain one contrast image per block, quantifier, and condition for the second-level group analysis. In particular, proportions below 40% (20, 30) and above 40% (50, 60, 70) were collapsed into one contrast image for each block and quantifier in order to keep the design matrix estimable with 15 rows and 15 columns (instead of an underspecified matrix with 30 columns).

At the second level, a flexible factorial model was run that allowed comparing the critical proportion "40%" to these contrast images for proportions lower or higher, separately for each quantifier and block. According to our hypothesis, we tested for a general change in activation from the baseline block to the testing block for the trained as well as the untrained quantifier. This was done separately for "many" and for "few", with a subsequent conjunction analysis assessing the commonalities in signal change in both quantifiers. Effects are reported at p < .05 family-wise error (FWEc) corrected at cluster level if not indicated otherwise.

Next, in order to test for specific effects at the novel criterion "40%", the signal intensity for this proportion was compared to that of the proportions above 40% separately for blocks 1 and 3, thus assessing the interaction contrast of PROPORTION and BLOCK. These effects were tested within a region of interest defined by the thresholded contrast of the previous conjunction analysis defining the overall effect space. Moreover, in analogy to the analysis of the behavioral data, the 3-way interaction with QUANTIFIER was also assessed.

3. Results

3.1 Behavioral effects

The 2×2×6 ANOVA yielded significant main effects for BLOCK (F[1,16] = 15.32; p = .001) and PROPORTION (F[5,12] = 5.40; p = .007), and QUANTIFIER (F[1,16] = 20.53; p < .001). Moreover, all two- and three-way interactions were significant (QUANTIFIER x BLOCK: F[1,16] = 8.72; p = .009; QUANTIFIER x PROPORTION: F[5,12] = 59.04; p < .001; BLOCK x PROPORTION: F[5,12] = 7.48; p = .002; BLOCK x QUANTIFIER x PROPORTION: F[5,12] = 4.14; p = .020).

At the critical proportion 40%, the 2×2 ANOVA yielded significant main effects for BLOCK (F[1,16] = 5.13; p = .038) but no effect for QUANTIFIER (F[1,16] = 3.33; p = .

087). Moreover, there was a significant interaction of QUANTIFIER x BLOCK (F[1,16] = 17.08; p = .001). Post-hoc t-tests revealed that there was an adaptation effect for both quantifiers ("many": t[16] = 4.34; p = .001; "few": t[16] = 2.38; p = .030; all tests one-tailed and Bonferroni-corrected) which was numerically larger for the trained quantifier "many" than for the not trained quantifier "few". These effects had opposite directions, i.e. there was an increase in acceptability for "many" and a decrease for "few" in the test block relative to the baseline block. In other words, there was a pronounced learning effect for "many" reflected in the increasing tendency in Block 3 to call 40% of circles of the named color "many" while at the same time the likelihood to call this proportion "few" decreased.

3.2 fMRI effects

3.2.1 Overall adaptation over the course of the experiment—The whole-brain analysis of the overall task-related activation yielded a network for quantifier processing that covered bilateral inferior frontal, postcentral/inferior parietal including bilateral intraparietal sulcus, and occipital areas (Figure 2, panel a, areas colored in yellow; cluster-level family-wise error corrected p < .05 effected as p < .001 uncorrected, extent k = 205 voxels). The reverse contrast (block 3 minus block 1) yielded no significant effects in the whole-brain analysis. Subsequently, we analyzed training effects in the brain in terms of changes from the baseline block to the testing block. Separate analyses for the trained quantifier "many" and the not trained quantifier "few" revealed a significant signal decrease for both quantifiers in Block 3 compared to Block 1 (Figure 2, blue and red blobs). The conjunction analysis of both contrasts revealed the change of activation level common to both contrasts yielded one cluster of 576 voxels solely confined to the left inferior frontal cortex (Figure 2, panel a, violet blob). The blob covered parts of both BA 44 (193.3 voxels = 33.6% of the cluster; 21.3% of BA 44 activated) and BA 45 (38 voxels = 6.6% of the cluster; 5.2% of area 45 activated). The family-wise error corrected p < .05 at cluster level was effected by an uncorrected p < .001 threshold in combination with an extent threshold of k = 350 voxels

3.2.2 Specific learning effects in Broca's region—Next, we assessed whether there was a specific training effect for the critical proportion "40%", i.e. whether the relative change in activation from the baseline block to the test block at proportion "40%" was more pronounced than that for the higher proportions for which no learning occurred. The analysis was confined to the regions described above that generally revealed a change of activation during the course of the experiment, thus revealing which parts of the so far observed changes were specific to training and not due to e.g. overall adaption or order effects.

The respective interaction effects are reported in Table 1 and illustrated in Figure 4. For BA 44, we observed stronger effects for proportion "40%" than for the control larger proportions. These specific adaptation effects were comparable for both the trained quantifier "many" and the untrained quantifier "few," as indicated by the non-significant interaction. In contrast, in BA 45, there was a stronger specific effect for proportion "40%" for the trained quantifier "many" than for the control proportions (i.e. proportions above 40%), and an absence of such a specific effect for "few", thus constituting a significant three-way interaction of PROPORTION x BLOCK x QUANTIFIER.

4. Discussion

The present study investigated how the brain represents words with flexible meaning such as quantifiers. In particular, we were interested to reveal the neuroanatomical basis for flexible adaptations in quantifier semantics. To this end, we applied a novel learning-adaptation paradigm tested previously in a set of behavioral studies. Behavioral data replicated these earlier findings. With respect to the fMRI data, in accordance with our hypothesis, left inferior frontal cortex was of central importance. Analysis of adaptation changes yielded overall activation decrease in areas 44 and 45 in Broca's region that were common for all proportions. Most importantly, in both areas there were also specific effects for the critical proportion "40%." Here we found relative activation increases in comparison to the other proportions and were thus opposite to the general adaptation effect. These findings will now be discussed in more detail.

Judgments of quantifiers seem to involve a mechanism for representing quantity knowledge in the parietal lobe and a decision-making mechanism in dorsolateral prefrontal regions. This replicates previous fMRI work (Troiani et al, 2008; McMillan et al, 2005; Heim et al., 2012) and patient studies (e.g. Troiani et al. 2011; Morgan et al. 2011; McMillan et al. 2006) demonstrating the complex role of multiple brain regions in the representation of the meaning associated with a very common segment of the vocabulary. However, the representation of the meaning of words like "many" and "few" can be quite variable and often depends on the context in which these words are used. Despite an a priori sense of the meaning of these words, as we showed in the behavioral studies, this meaning can shift to accommodate the context of their use, and the new meaning can be represented reliably. This is different from the less flexible representation of object concepts and action concepts that are more dependent on sensory-motor features in modality-specific association cortex (e.g. Fernandino et al., 2015; Thompson-Schill, 2003; Martin, 2007).

In this study, we sought to determine the neuroanatomic basis for the process of modifying the flexible representation of word meaning. The core finding of the study can be summarized as follows: Whereas some overall learning took place in the course of the experiment, which was present both in the behavioral data and in the fMRI data in BAs 44 and 45, a second, more specific learning process happened on top of the general effect. This specific effect was observed for the critical proportion "40%." Our two observations were: (1) a relative signal increase (as compared to the signal for higher proportions) from block 1 to block 3 in association with acquiring new criteria related to "many" and "few" as opposed to the overall decrease over time, and (2) a partly differential involvement of BA 44 and 45 in Broca's region.

The involvement of left BA 45 in specific adaptation of quantifier meaning was expected in the hypothesis, since it is in accordance with the literature on semantic processing in general (e.g. Amunts et al. 2004; Binder et al., 2009; Heim et al. 2009; Newman et al. 2010). Detailed studies assessing the acquisition of a new word have shown recruitment of BA 45 as well (Koenig et al., 2005, 2007). Moreover, activation of BA 45 has been observed previously during the processing of quantifier semantics (Heim et al. 2012; McMillan et al. 2005; 2013; Wei et al. 2012). The pattern of the fMRI data in BA 45 reflects the behavioral

data in the present study as well as in the previous behavioral studies (Heim et al. 2015). In these three experiments, the direct adaptation effect for the trained quantifier was always stronger than the indirect adaptation effect for the not trained quantifier. Similarly, in the present fMRI data, the direct adaptation effect in area 45 was greater for the trained quantifier "many" than the indirect adaptation effect for the not trained quantifier "few". This obvious correspondence between the semantic learning effect in the behavioral data and the level of activation in BA 45 underscores the interpretation of the role of BA 45 as a region contributing to the flexible representation of meaning in the context of quantifier processing. The observation that BA 45 is sensitive to the adaptation of flexible meaning in a quantifier learning task is in line with a wealth of other language studies that have implicated BA 45 in a variety of semantic contexts (e.g. Amunts et al. 2004; Binder et al., 2009; Heim et al. 2009; Newman et al. 2010; Koenig et al, 2007).

Left BA 44 also was engaged in the task of processing the flexible meaning of these quantifiers. This was true for both the explicitly trained quantifier "many" and the other quantifier "few" that had never been mentioned in the training phase. For both quantifiers there was a relative increase of activation in the contrast of the trained proportion "40%" in comparison to the higher proportions (Figure 3). These findings are in line with a series of studies by Badre and colleagues (e.g. Badre et al. 2010; Badre & D'Esposito, 2007; Badre & Frank, 2011) who consistently found learning-related effects in very close vicinity to the coordinates in superior BA 44 reported here. In contrast to other studies focusing on the anterior part of the inferior frontal gyrus including BA 45 (see also Wagner et al., 2014), these effects were not explicitly semantic in nature but expressed processing success in reinforcement learning of hierarchies. This paradigm resembles the one used in the present study in two relevant aspects: the application of explicit reinforcement and a component of abstract rule learning (as opposed to learning of pair associates). Other studies (e.g. Thompson-Schill et al., 1997; Heim et al., 2007) discussed the role of BA 44 in terms of explicit and implicit selection mechanism in linguistic contexts. It could thus be that, in line with earlier reports of a functional parcellation of Broca's region during quantifier processing (e.g. Heim et al. 2012), areas 45 and 44 in Broca's region fulfill partly distinct functions: Area 45 as a semantic region and area 44 as a region for response selection on the basis of certain rules. However, since the present study was not designed to test such a functional distinction, future work is necessary to address this issue. For the purpose of the present study, it is important that the initial hypothesis, i.e. the involvement of BA 45 in Broca's region in the semantic re-evaluation of flexible quantifier meaning, could be confirmed.

Finally, in contrast to this signal increase that was specific for the critical proportion "40%" reflecting a selective re-interpretation of proportion "40%" as "many" (Figure 3), there was also a general signal reduction over time. This effect was common to all proportions and quantifiers. It might thus be thought to reflect the overall adaptation of the subjects to the task setting and the required decisions (e.g. Derrfuss et al. 2005), which might be due to an order effect of blocks. Interestingly, it was also located in Broca's region as part of the general quantifier processing network (Figure 2). This effect has been attributed to increasing efficiency of a neuronal population, adaptation, and other related phenomena where reduced levels of activation are seen to accompany experience with a set of stimuli

(Buckner et al., 1998; Grill-Spector & Malach, 2001; Kourtzi & Kanwisher, 2001; Santi & Grodzinsky, 2010). In this experiment, we did not include an extra control for order effects; future studies may use ABAABA designs instead of the simple ABA design used here to be better able to isolate order effects.

5. Conclusion

The present study used a novel linguistics-based paradigm to test the hypothesis that a flexible adaptation of the meaning of a word (in this case, a quantifier) is supported by BA 45 in left inferior frontal cortex. The data add to our understanding of the function of this part of Broca's region. They also add a neurofunctional perspective on the basis for the flexible representation of quantifier meaning (for a formal perspective cf. Gierasimczuk, 2007; for a developmental perspective and the distinction of quantifiers and numbers see Hurewitz et al. 2007; for a decision-making perspective cf. Gold & Shadlen 2007). Words with flexible meaning like quantifiers can be used in context-specific situations to emphasize a particular attribute of the context, and our findings suggest that left inferior frontal cortex plays a crucial role in this process. The present study demonstrating the neural basis for semantic flexibility in quantifier processing may thus serve as a basis for more specific basic and also applied clinical research questions in the future.

Acknowledgments

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Highlights

- The meaning of quantifiers (e.g. "many") can be changed.

- This change translates to other quantifiers.

- Left BA45 is crucial for the re-interpretation of quantifier semantics.
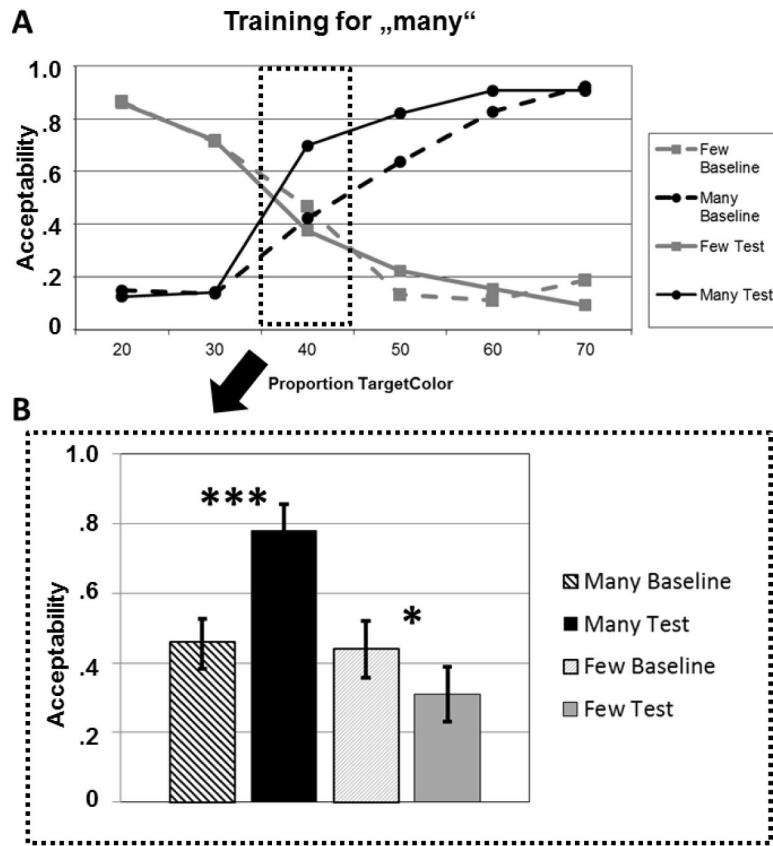
Figure 1.
A. Average acceptability ratings for a given proportion of circles of the mentioned color, plotted separately for the quantifiers *"many"* (black lines) and *"few"* (gray lines) in the baseline blocks (dashed lines) and the test blocks after adaptation (solid lines). B. Average acceptability ratings for a critical proportion of circles of the mentioned color, plotted separately for *"many"* (black bars) and *"few"* (gray bars) in the baseline blocks (dashed bars) and the test blocks after adaptation (solid bars), reveal significant changes for both quantifiers (* p < .05; *** p < .001).
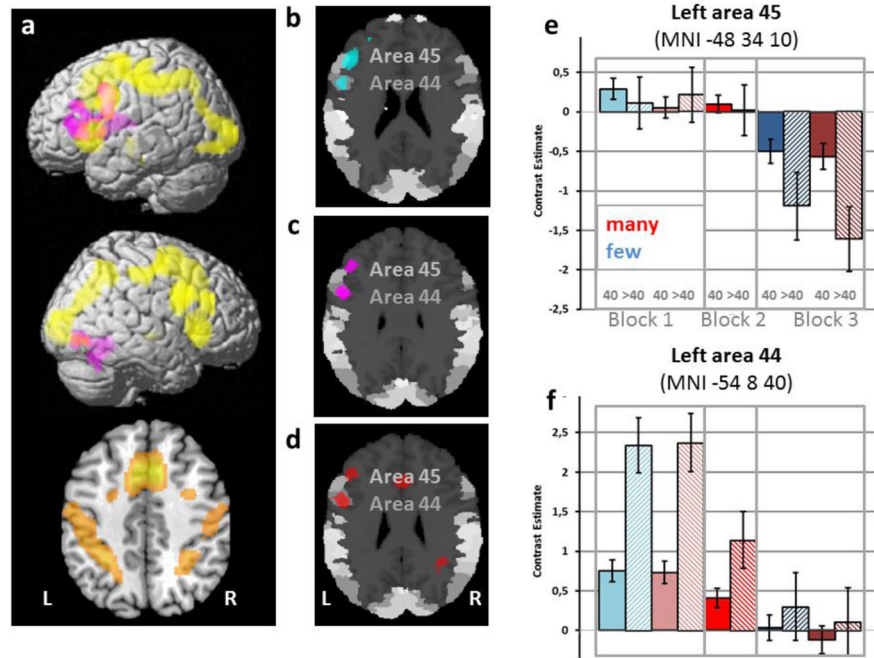
Figure 2.
[a] The quantifier processing network (yellow) in the left and right hemisphere and overall training-induced changes (violet). *[b–d]* Training-induced changes in the left inferior frontal cortex, plotted separately for the trained quantifier "many" (red, panel d), the not trained quantifier "few" (blue, panel b), and the conjunction of both effects (violet, panel c). *[e–f]* Bar graphs indicate the contrast estimates obtained from the random-effects group analysis for the critical proportion "40%" (40) and the higher proportions (>40) as a function of block (block 1, 2, 3) and quantifier, separately for the local maxima (cf. MNI coordinates) in areas 45 *[e]* and 44 *[f]*. All blobs at family-wise error corrected p < .05 at cluster level. See also Figures 3 and 4 for further analyses.
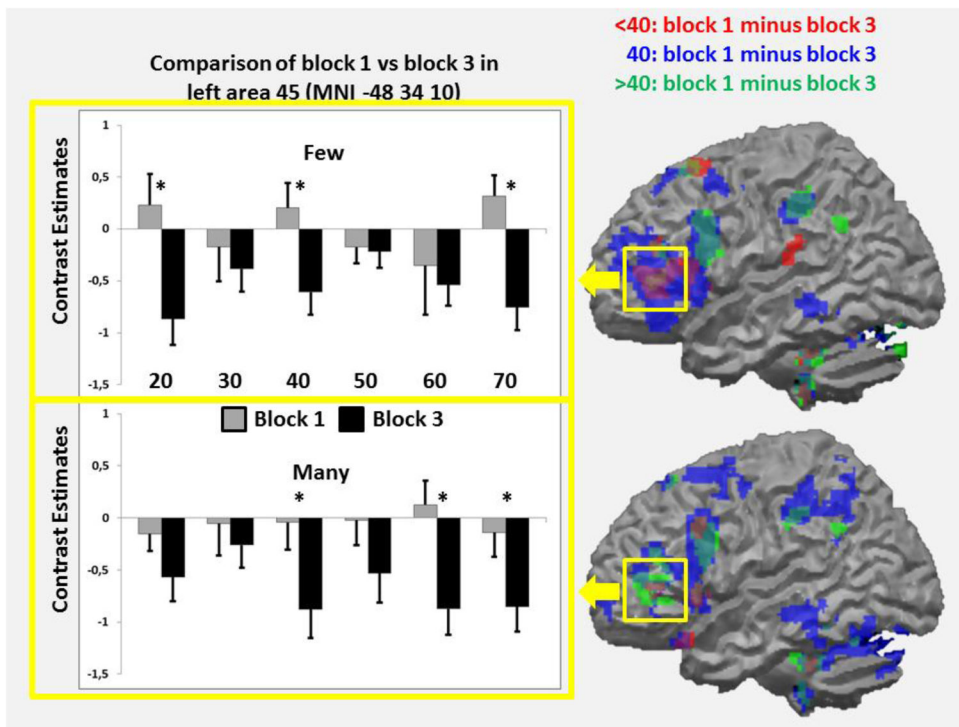
Figure 3.
Left: Contrast estimates extracted from the individual conimages per subject, plotted separately for each proportion as a function of quantifier (upper panel: *Few*; lower panel: *Many*) and block (gray: baseline block 1; black: test block 3). The bars reveal the overall numerical adaptation for each proportion and quantifier. Significant differences are highlighted (* p < .05 two-tailed t-tests). Right: Separate whole-brain maps for the adaptation effects block 1 minus block 3 for proportions <40, 40, and >40 (p < .001 uncorrected, k 30 voxels).
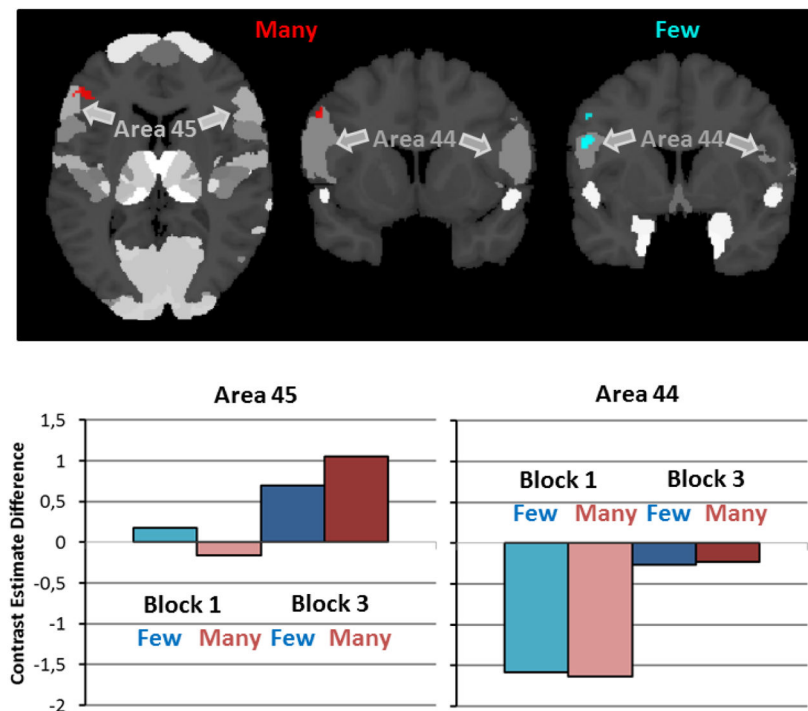
Figure 4.
Significant two-way interactions of BLOCK (block 1, block 3) and PROPORTION (40, greater than 40) after training for "many" as a function of quantifier and cytoarchitectonic area. TOP: Red indicates the interaction effect for the trained quantifier "many". Blue indicates the interaction effect for the not trained quantifier "few". All clusters displayed at p < .001 uncorrected, k 20 voxels (note that for "Few" there was no significant effect in area 45 cf. Table 1). BOTTOM: Specific effects for the trained proportion "40%", expressed as bar graphs of the difference of the contrast estimates for proportion "40%" minus those for proportions greater than "40%" (i.e. the differences between the bars depicted in Figure 2 for each quantifier and block). Note the relative increase for both quantifiers, and especially for the trained quantifier "many", from baseline block 1 to testing block 3 in area 45 (left graph) and. Note also the relatively comparable increase in area 44 (right graph) for both trained and untrained quantifier from block 1 to block 3.

Table 1

Interaction of experimental conditions in areas 44 and 45 (Amunts et al. 1999) in Broca's region. Non-significant effects (*p > .05*) printed in Italics.

	Left area 44 (−54 8 40)		Left area 45 (−48 34 10)	
Interaction term	t(210)	p	t(210)	P
"Many": BLOCK x PROPORTION[1]	3.69	< .001	3.35	< .001
"Few": BLOCK x PROPORTION[2]	3.76	< .001	1.55	.061
QUANT x BLOCK x PROPORTION[3]	.27	.394	2.14	.018

[1](Many3_40 > Many3_gt40) > (Many1_40 > Many1_gt40)

[2](Few3_40 > Few3_gt40) > (Few1_40 > Few1_gt40)

[3][(Many3_40 > Many3_gt40) > (Many1_40 > Many1_gt40)] > [(Few3_40 > Few3_gt40) > (Few1_40 > Few1_gt40)]