Behavioral and neural effects of training and word class in object and action naming in healthy subjects

Evidence from fMRI

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Abstract

Word retrieval deficits are a common problem in patients with stroke-induced brain damage. While the complete recovery of language in chronic aphasia is rare, patients' naming ability can be significantly improved by speech therapy. A growing number of neuroimaging studies have tried to pinpoint the neural mechanisms associated with successful outcome of naming treatment. Although the picture is complicated by the large variability in lesion and patient characteristics, some advances have been made in this direction. However, one piece of the puzzle is missing. Namely, the brain mechanisms supporting naming practice in the healthy brain have not received enough attention. Yet, understanding these mechanisms is crucial for teasing them apart from functional reorganization resulting from brain damage.

In this thesis I present an fMRI study of intensive naming practice in healthy monolingual adults. Subjects were trained on naming objects and actions from pictures for ten consecutive days and were scanned twice, before and after training. Training of noun and verb production was associated with a similar set of BOLD activation changes, encompassing both anterior and posterior regions of the left hemisphere. Interestingly, while the anterior regions (posterior inferior frontal gyrus, anterior insula, anterior cingulate cortex) showed significant practice-related BOLD decreases, activity in the posterior regions (precuneus, posterior cingulate cortex, angular gyrus, posterior middle temporal gyrus) increased following training. We argue that while the activation decreases were likely associated with the facilitation of different aspects of word production, the greater engagement of parietal and temporal cortices after training potentially reflects retrieval of knowledge pertaining to trained items from episodic (and potentially semantic) memory. Additionally, using the data from the pre-training fMRI session, we investigated the putative dissociation between neural representations of nouns and verbs. In line with previous reports, we found that action naming recruited bilateral lateral occipitotemporal and posterior parietal and inferior frontal cortices (predominantly left-lateralized) to a greater degree than object naming.

Our second experiment aimed to further scrutinize categorical distinctions in lexical representation by tackling the effects of verb transitivity. Corroborating previous findings, we observed greater recruitment of several regions in a fronto-temporo-parietal network for transitive verbs. However, in alternative to previous reports that accounted for the results in terms of linguistic processes, we interpreted the observed effects in terms of perceptual and conceptual differences between transitive and intransitive verbs. We outline the major questions that should be addressed by future studies.

From the methodological perspective, we validated the use of a recently introduced multivariate searchlight pattern classification method for the analysis of training effects in language studies. We found that, compared to the standard GLM method, the searchlight analysis has comparable and, in some cases, greater sensitivity in localizing BOLD signal changes, and thus it represents a promising complementary tool in studies of training.

Chapter 1. General introduction

Attempted naming can improve performance in individuals with aphasia even in the absence of feedback or corrections (Howard, 2000; Nickels, 2002). However, the neural mechanisms underlying this facilitation are not clear. The investigation of factors contributing to anomia recovery in individuals with language disorders is complicated by large variability in size and location of lesions, as well as by individual patient characteristics. Neuroimaging studies in patients with aphasia suggest that homologous right-hemispheric regions may show increased blood-oxygenation-level dependent (BOLD) activation in comparison to healthy controls. This observation has been deemed consistent with the view that these regions may take over damaged left hemisphere functions, at least to some extent. However, whether this “takeover” is compensatory (Meinzer et al., 2006; Vitali et al., 2007) or maladaptive (Postman-Caucheteux et al., 2010) is still a matter of debate.

Recently, the argument has been put forward that neural mechanisms underlying improvement in anomic patients can partially overlap with those that support naming facilitation in the healthy brain (Heath et al., 2015; Kurland et al., 2018). Thus, it is necessary to establish a “baseline” of practice-induced changes in control subjects, against which the results of anomic patients could be compared.

So far, most studies with healthy individuals have focused on the effects of incidental naming practice, during which stimulus repetitions were scarce and implicit (e.g., van Turennout et al., 2000, 2003; Meister et al., 2005). Findings suggest that even a single instance of naming in the context of a picture naming task can yield long-lasting changes in processing of a stimulus, which can persist for days and even weeks. Whereas behaviorally this effect corresponds to shorter naming latencies, at the neural level it is reflected by decreased activity in bilateral occipitotemporal and left prefrontal cortices, associated with facilitated perceptual/conceptual and linguistic processing of the stimulus, respectively.

An intensive naming training paradigm, more closely resembling speech therapy in patients, was recently introduced by Basso and colleagues (2013). They found that explicit object naming practice over the course of ten consecutive days was associated with deactivation of the left inferior frontal cortex and the fusiform gyrus, in line with reports of primed naming studies, and at the same time resulted in hyperactivation of medial parietal areas, not involved in the classic language circuit.

In **Chapter 2** we provide a review of the existing investigations of practiced naming in healthy individuals. Available studies discuss how practice-related activation changes can be modulated by a number of factors, including the intensity of practice, the time elapsed between stimulus repetitions, and the coherence between the encoding phase and the task used to measure the effects of practice.

Yet, one such factor, namely, the content of training, has received undeservingly little attention. Most studies so far have focused on practiced naming of common objects that are referred to by nouns. Neuropsychological findings with patients (for review, see Mätzig et al., 2009), as well as recent neuroimaging studies with healthy individuals (for reviews, see Crepaldi et al., 2011, Vigliocco et al., 2011), suggest that words belonging to different grammatical classes, such as nouns and verbs, may have at least partially dissociable neural correlates. Thus, it seems reasonable that they are differently affected by practice.

To our knowledge, only one neuroimaging study has explicitly addressed a potential interaction between the effects of naming practice and the contents of practiced material, by including words from both grammatical classes in their experimental paradigm (Kurland et al., 2018). The analysis of response latencies collected in the scanner suggested that practice-related naming facilitation was greater for verbs than for nouns. However, fMRI data did not corroborate an interaction between training and word class effects in any of the analyzed regions. It should be noted that despite the superficial similarity to Basso et al.'s two-session training study, practice in Kurland et al.'s study was less intensive (five repetitions a few days prior to fMRI, plus five repetitions immediately before the scanning). Thus, the lack of significant interaction effects could have stemmed from an insufficient number of repetitions. This and other accounts are discussed in this Chapter.

In **Chapter 3** we present the results of the fMRI study of intensive naming practice, in which we investigated the potential differences in the magnitude and localization of training effects observed for nouns and for verbs. To this end, we replicated the training paradigm introduced in Basso et al. (2013) with healthy speakers of Italian who practiced simultaneously on naming of objects and actions for ten consecutive days and were tested (either in the fMRI scanner or behaviorally) twice — on the days preceding and following the training. The two experimental sessions were identical and included items that were subjected to training, as well as an equal number of untrained items that were used as control for task habituation and priming effects.

The use of this paradigm allowed us to simultaneously tackle several questions.

First, we investigated the effects of training and their potential interaction with word class, by comparing trained and untrained items within and across sessions. We argue that establishing the correlates of intensive naming practice in healthy individuals could help interpret neuroimaging data obtained from anomic patients, and allow us to tease apart the normal processes evoked by repeated naming from the plasticity arising as a result of compensatory mechanisms. It could also potentially help identify regions that can serve as predictors of naming therapy success, thus allowing for better prognosis of treatment outcome.

Second, by looking at the activation changes associated with a single repetition of nouns and verbs that did not partake in training over the course of two weeks we could test the presence of long-term priming effects reported in previous studies (Meister et al., 2005; Meltzer et al., 2009) and set them apart from the effects of explicit training.

Finally, the availability of “baseline”, pre-training data provided us with an opportunity to scrutinize the brain networks involved in naming of objects and actions and to contribute to the ample research on putative distinctions between the neural representations of nouns and verbs.

In the second experimental study, described in **Chapter 4**, we continued to examine the categorical effects of word processing by probing subtler distinctions in lexical representations of verbs. Namely, we focused on the investigation of the neural correlates of verb transitivity. Argument structure of a verb, and, in particular, the number of thematic roles (arguments) it can assign, is a prominent feature of verb processing. While defining the syntactic frame around which a sentence is built, it simultaneously contributes to verb semantics by encoding the information about the participants of an action/event. Clinical research shows that individuals with aphasia experience more difficulties with transitive than intransitive verbs (Dragoy & Bastiaanse, 2010; Kim & Thompson, 2000, 2004). The neural underpinnings of such difficulties, and the neurofunctional substrate of the distinction between transitive and intransitive verbs, are still a subject of debate. Neuroimaging findings suggest that different aspects of argument structure processing are supported by a widely distributed network, encompassing several temporoparietal regions, as well as Broca's area (for review, see Thompson & Meltzer-Asscher, 2014), but extant evidence is contradictory. In our experiment we aimed to investigate the neural underpinnings of transitivity effects in young healthy individuals using a picture naming task.

The thesis is concluded by **Chapter 5**, which provides a summary of our findings and puts them into a larger perspective. There we discuss how studies of cortical concept representations and of neural mechanisms underlying word production, that have been mainly progressing in parallel, could shed more light on both "object vs. action" and "noun vs. verb" dichotomy, if they paid more consideration to the knowledge accumulated by each other. We also argue that the recent paradigm shift in neuroscience from modular to network approach could help us gain a better understanding of the underlying mechanisms of functional brain plasticity associated with language training.

Chapter 2. Neural correlates of naming practice: From repetition priming to explicit training

1. Introduction

Folk wisdom says that practice makes perfect. While the truthfulness of this statement might seem trivial, brain mechanisms accompanying practice-related facilitation are still not fully understood. Converging evidence from studies in various domains suggests that behavioral improvement on a task is associated with long-lasting, and potentially even permanent, changes in brain function, a phenomenon often referred to as *functional plasticity* (Grafman, 2000; Poldrack, 2000).

In the domain of language, long-term functional plasticity in healthy monolingual subjects has been studied in the context of tasks as diverse as grammar learning (Musso et al., 2003; Opitz & Friederici, 2003; Kepinska et al., 2018), practicing novel morphological inflection (Nevat et al., 2017), vocabulary acquisition (Breitenstein et al., 2005), and learning to discriminate between new phonological contrasts (Callan et al., 2003) and tones (Wang et al., 2003). Another line of research has focused on modifying the neural representations of pre-existing linguistic knowledge by incidental or explicit practice.

In the present review we will provide a summary of the neuroimaging studies investigating brain correlates of naming practice, and will discuss how their findings could contribute to the refinement of the existing models of practice-induced plasticity.

2. Review of the studies of practiced naming

2.1. Behavioral and neural correlates of priming

Prior exposure to a stimulus can facilitate its subsequent processing, which in the laboratory setting is reflected by improved accuracy and faster reaction times (RTs). This facilitation, known as *priming*, is believed to rely (primarily) on implicit memory and to function independently from the conscious recollection of a stimulus, as evidenced by intact priming effects in amnesiac patients with medial temporal lobe damage (Warrington & Weiskrantz, 1974; Graf et al., 1984). The double dissociation between the two forms of memory is further supported by accounts of patients showing the opposite dynamics — i.e., impaired priming in the presence of intact episodic memory (Gabrieli et al., 1995). Additional evidence comes from the comparison of performance on "direct" (explicitly requesting prior knowledge of a stimulus) and "indirect" (not containing explicit instructions to use prior knowledge) tasks in healthy individuals (Tulving et al., 1982), as well as the ability of subliminally-presented (and thus not consciously processed) stimuli to evoke priming effects (Forster & Davis, 1984).

Behaviorally, the effects of repetition priming can be very long-lasting. For example, picture-naming latencies were reported to show robust priming effects over periods of 6 weeks (Mitchell & Brown, 1988), 48 weeks (Cave, 1997) and 22 months (Maylor, 1998). More strikingly, according to Mitchell (2006), nonconscious priming can persist for over a decade: subjects who were exposed to object drawings three times in one laboratory session, were significantly better at identifying these objects from depicted fragments 17 years later, as compared to a control group of subjects who did not participate in the priming session. In a recently published longitudinal study, Mitchell et al. (2018) extended their previous results by comparing the long-term priming effects (11-14 years) across a number of tasks. In particular, they found significant priming on picture fragment identification and word fragment completion tasks, but no priming on word stem completion or category exemplar generation[1]. This dissociation suggests that such extreme longevity (years and even decades) can be characteristic of perceptual, but not conceptual, priming[2].

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[1] In category exemplar generation tasks, participants need to generate a certain number of exemplars belonging to a given category in a limited period of time. Word stem completion task consists in completing the presented "word stems" (the initial three-four letters) with the first word that comes to mind. For word fragment completion and picture fragment identification, subjects are asked to identify the previously seen words/pictures from their fragments.

[2] Although in the early days of priming research word stem completion was considered a purely perceptual task, recent findings suggest that, in contrast to word fragment identification task, it taps into conceptual knowledge (e.g., Soler et al., 2015). For an elaborate taxonomy of perceptual and conceptual priming tasks, see Bruss & Mitchell (2009).

The most likely neural counterpart of priming is the phenomenon of *repetition suppression*. Single-cell recordings in macaque monkeys revealed a decrease in the firing rate of neurons of the inferior temporal cortex in response to repeated stimuli. This effect could be observed already after a single exposure to a stimulus and persisted for minutes (Desimone, 1996).

Although the techniques applied to human subjects have a much lower spatial resolution and do not allow direct measures of neuronal activity, a considerable amount of evidence comes from studies examining hemodynamic changes in the brain using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET). Most commonly, a decrease in blood flow, also referred to as *repetition suppression*, is observed for primed as compared to unprimed stimuli in the areas initially involved in a task (for review, see Henson, 2003). However, under certain conditions the opposite phenomenon is reported — namely, increased activation in response to a primed stimulus; this effect is sometimes referred to as *repetition enhancement* (for review, see Segaert et al., 2013).

Probably the most extensive research of repetition suppression effects has been conducted in the framework of the fMRI adaptation paradigm, introduced by Grill-Spector and colleagues (1999). In this paradigm, researchers consecutively present two stimuli differing from each other in some perceptual property (such as view angle), and if the second stimulus shows repetition suppression, or *adaptation*, in a certain area, this area is considered to be “indifferent” to a manipulated property (in the example above, view-independent). Studies of semantic priming (e.g., Rossell et al., 2003; Kotz et al., 2002) follow a similar logic: they investigate the modulation of response to a word (*target*) which is directly preceded by another word (*prime*) that shares with it some semantic property. However, the adaptation effects stemming from back-to-back stimulus presentation are known to be very brief and might not even survive an intervening item (Henson, 2003); thus, they most likely do not reflect lasting changes in the functional brain organization. For this reason, these studies will not be discussed in detail in the present review. Instead, we will focus on the evidence of neural repetition effects spanning over periods of hours, days and even weeks.

2.2. First studies of primed picture naming: the effects of repetition lag and number of repetitions

Behavioral studies of perceptual priming converge on the conclusion that even a single exposure to a visual stimulus can facilitate its subsequent processing for long periods of time, ranging from minutes to years. Evidence from PET and fMRI studies of object priming suggests that this facilitation is typically accompanied by decreased activation, or repetition suppression, in occipitotemporal areas (Badgaiyan, 2000; for review, see Schacter & Buckner, 1998).

These findings could be of relevance for the interpretation of long-term priming effects observed in picture naming that manifest themselves as shorter response latencies in healthy individuals (Cave, 1997) and improved accuracy ratings in aphasic patients (Nickels, 2002). However, following the initial picture recognition, object naming engages a number of higher-order linguistic processes (Levelt et al., 1999) which are mediated by a broad network of brain areas (for reviews, see Indefrey & Levelt, 2004; Price, 2012). Thus, it is not obvious whether the modification within the perceptual or the language network contributes to the behavioral facilitation. Indeed, several studies of perceptual priming reported that repetition of familiar objects was accompanied by reduced activation in language-related areas, including the left inferior frontal cortex (Buckner et al., 1998; Buckner et al., 2000; Koutstaal et al., 2001; Vuilleumier et al., 2002; Simons et al., 2003), potentially due to automatic covert naming of the presented objects. Thus, several mechanisms can simultaneously contribute to the priming effects in picture naming (Francis, 2014; Francis et al., 2008; Bruss & Mitchell, 2009).

The first study to directly assess the neural effects of repeated object naming was carried out by van Turennout and colleagues (2000). Using the covert naming paradigm, they measured the short-term (30 sec) and long-term (3 days) effects of a single, brief (200 ms) repetition of real and nonsense objects. Subjects were instructed to name real objects and passively view nonsense objects. The imaging data were collected in a single fMRI session that included pictures primed three days prior to the scanning, as well as novel items that were presented twice during the session with an interval of 30 seconds. Thus, responses to three types of events — “novel”, “30-second delay” and “3-day delay” — could be directly compared. The analysis of priming effects at both repetition lags was masked by the areas initially involved in object recognition/naming, as identified by contrasting real and nonsense objects with the visual noise baseline. The results revealed that the BOLD signal in the occipitotemporal cortex, including bilateral occipital and fusiform gyri, decreased significantly 30 seconds after the initial stimulus presentation. Though the deactivation was strongest in the short-term priming condition, it could still be detected 3 days later. Importantly, effects of comparable magnitude were observed in the occipital regions for nameable (real) and non-nameable (nonsense) objects, consistent with the role of these regions in the extraction of low-level shape features that precedes object recognition (Malach et al., 1995; Kourtzi & Kanwisher, 2001). At the same time, two regions in the left hemisphere, including the inferior frontal gyrus (IFG) and the anterior insula[3], showed priming-related changes that were immediate, but grew stronger over the course of 3 days. Interestingly, these changes were in opposite directions — while the BOLD amplitude in the IFG decreased as a function of time, it increased in the insula. The fact that the changes in anterior brain regions were restricted to nameable objects was attributed by the authors to their association with linguistic priming, namely, facilitated lexical retrieval and/or phonological encoding. This interpretation seems plausible, considering that the deactivations were restricted to Broca’s area — the portion of the left inferior frontal cortex commonly implicated in various aspects of language processing. Additional evidence of time-dependent interaction between the insula and the inferior frontal cortex comes from a PET study by Raichle et al. (1994), who reported similar dynamics in these areas following brief practice (10-15 min) on a verb generation task, suggesting that, as a result of experience, lexical retrieval becomes less dependent on the left IFG and is at least partially taken over by the insula. Taken together, different time course and direction of the effects in anterior and posterior brain regions suggest that two distinct mechanisms may mediate long-lasting priming of picture naming.

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[3] While the precise anatomical labels for active clusters were not provided in the paper, the left IFG deactivations at both delays seem to be circumscribed by the pars triangularis (BA 45)/pars opercularis (BA 44); the insular activation peaks likely correspond to the precentral gyrus of the insula.

In order to further investigate the dynamics of cortical activity in the object naming system as a function of time and experience, van Turennout and colleagues (2003) compared the effects of a single and of multiple repetitions at different time intervals using a similar paradigm. Stimuli were either repeated once – at a 30-second, 1-hour, 6-hour or 3-day delay, or were presented four times in total – with a short (30 sec between exposures) or a long retention interval (with repetitions 3 days, 6 hours and 1 hour after the initial presentation). While a single repetition evoked activation changes consistent with the findings of the previous study (with the basal ganglia additionally showing the priming-related BOLD increase in both conditions), only bilateral occipitotemporal cortices and the left IFG were sensitive to the number of repetitions. However, whereas occipitotemporal areas showed reduced activation following four exposures, as compared to one, both in the long-term and short-term condition, activity within the left IFG declined only if the repetitions were spaced out over the course of three days. The increase within the insula and the basal ganglia was equivalent following multiple repetitions at both delays. These findings confirm the dissociation between the two neural systems involved in priming of object naming, with posterior areas most likely involved in perceptual priming, and anterior areas associated with facilitated language processing. Data suggest that the magnitude of practice-related changes in anterior regions is modulated as a function of time (effect of the repetition lag) and experience (effect of the number of repetitions).

As noted above, behavioral priming effects are known to persist for even longer periods of time. For example, in Mitchell & Brown's experiment (1988) facilitation of picture naming was stable across 1 to 6 weeks. Neural changes associated with such long-term priming were investigated by Meister and collaborators (2005), who compared the effects of repeated object naming at a1-day and a 6-week delay. The design of the study was very similar to van Turennout et al.'s (novel and repeated pictures were presented for 200 ms in an intermixed fashion); however, Meister et al. collected their data in two separate scanning sessions. In order to rule out the possibility that the differences in activation levels could be attributed to the variations in signal intensity across sessions or to task accommodation effects, Meister et al. included a set of novel, unprimed stimuli into both sessions, and confirmed that activations in response to them were indistinguishable at a very low threshold ($p<.1$, uncorrected)[4]. Behavioral effects of priming were stable across time, whereas conscious recognition of the pictures declined, as evidenced by follow-up subject debriefing. At a neural level, covert naming of novel pictures activated a broad network, extending from the bilateral occipital cortices to the left frontal regions. During naming of repeated stimuli, activations were significantly reduced in occipitotemporal areas and the left IFG at both delays; however, decreases in occipitotemporal regions that were initially spanning from the extrastriate to the posterior inferior temporal cortices, after 6 weeks were mainly restricted to the inferior temporal/fusiform gyri (BA 37). This agrees with the results of van Turennout et al. (2003), who found that the spatial extent of occipitotemporal decreases decayed over the course of several days. The inferior temporal cortex that showed long-term priming effects represents the endpoint of the ventral visual pathway (“vision for perception”, Ungerleider & Mishkin, 1982; Goodale & Milner, 1992) and mediates the storage of abstract, potentially amodal (Büchel et al., 1998; Fairhall & Caramazza, 2013), object representations. It seems, thus, that as sensory traces of previously processed stimuli in the low-level visual areas are weakened over time, potentially by interference from new visual information, long-term implicit memory of these stimuli is maintained in areas mediating their high-level representations in the ventral temporal cortex. In line with the previous reports, frontal regions also revealed priming-related repetition suppression. Namely, two clusters of the left IFG – in its posterior (pars opercularis/pars triangularis, BA 44/45) and anterior (pars orbitalis, BA 47) portions – showed the BOLD decrease after a 1-day delay; however, after 6 weeks deactivation was restricted to a small cluster in the anterior IFG. The left IFG has been implicated in a variety of language tasks across studies — from segmental phonology to syntax. Several studies suggested that while the posterior portion of the left IFG and the adjacent ventral precentral gyrus are responsible for phonological encoding, the more anterior regions mediate semantic retrieval (Wagner et al., 2000, 2001; Poldrack et al., 1999; Vigneau et al., 2006). Based on this proposed functional parcellation, Meister et al. suggested

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[4] This analysis was restricted to regions-of-interest defined as 3-mm spheres centered around the peak coordinates reported for the “primed vs. novel” contrasts by van Turennout et al. (2003).

that long-term priming in the anterior IFG could indicate permanent facilitation of semantic retrieval by repetition, in contrast to the transient priming of phonological forms.

2.3. Studies in healthy older adults: the role of task coherence and potential top-down priming mechanisms

In order to more closely investigate the involvement of language areas in primed naming over the course of minutes and days, MacDonald et al. (2015) examined a set of predetermined regions-of-interest (ROIs) in the left hemisphere, chosen based on language-related meta-analyses and their own previous work on repeated naming. In contrast to the above described studies that were interested in priming effects *per se*, this group had focused on investigating the substrates of naming practice as a potential means to inform our understanding of the mechanisms underlying successful treatment of word deficits in aphasic patients (Nickels, 2002). In accordance with this goal, they selected for participation a group of healthy older adults (mean age: 54.4 years) and adopted the practice paradigm that more closely resembled naming treatment in patients. Long-term facilitation was provided by asking subjects to name objects three times within each of the two separate behavioral sessions, one-two days prior to the scanning. Short-term practice involved repeated naming of objects that were previously presented once within the same scanning session (with 6-10 intervening trials and a maximum repetition lag of 2.5 min); the first of the two presentations in the scanner (“unprimed” condition) provided a baseline for comparison with items primed at both delays (“short-term” and “long-term” conditions).

The seven spherical ROIs included three subregions of the left IFG (pars orbitalis, pars triangularis and pars opercularis), along with a few temporal and occipital areas (posterior middle temporal, posterior superior temporal, posterior inferior temporal and extrastriate). The ROI analysis revealed significant practice-related deactivations exclusively within the three regions of the left IFG. However, the changes in different portions of the IFG followed distinct temporal dynamics: while only its most anterior region (pars orbitalis, BA 47) revealed immediate deactivation, all three ROIs in the IFG showed a significant BOLD decrease over the course of several days (and multiple repetitions). These findings are in line with van Turennout et al.'s (2000, 2003) hypothesis that practice-related changes in the frontal regions require a consolidation period to develop.

Based on functional distinctions within the left IFG proposed in the literature (Badre & Wagner, 2008; Wagner et al., 2000) and the theories of rostral-caudal abstraction gradient of the prefrontal cortex (Snyder et al., 2011), MacDonald and colleagues tentatively suggested that the long-lasting modulation of activity in the most anterior ROI, pars orbitalis (BA 47), may reflect immediate strengthening of the mapping between a stimulus and a concept (lemma), while decreases in more posterior pars triangularis (BA 45) and pars opercularis (BA 44) could be attributed to facilitated lexeme retrieval/selection and phonological encoding, respectively, which develop later.

While this explanation is plausible, it has to be noted that the design of MacDonald et al.'s study suffers from one significant flaw that complicates the interpretation of results. Namely, since items in the short-term priming condition were repeated only once, and items primed over the long term were repeated several times (total of six repetitions preceding the test exposure), the effects of repetition lag and number of exposures were inherently confounded. Thus, it cannot be completely ruled out that the more extended suppression observed in the left IFG in the long-term condition was at least partially due to more intense practice, rather than to the longer time elapsed between facilitation and testing.

Complementary whole-brain analysis detected repetition suppression in the pars triangularis and the inferior temporal gyrus bilaterally at a longer delay, consistent with the previous findings, as well as repetition enhancement in the bilateral precuneus both for the short-term and long-term conditions, potentially reflecting retrieval from episodic memory.

Probably the most surprising (non-)result of the study is the failure of both the ROI and the whole-brain analyses to detect any significant suppression in extrastriate cortices, expected with repeated visual object presentation. As proposed by the authors, this may be due to the methodological differences between their and previous studies, such as the choice of number of intervening trials (Sayres & Grill-Spector, 2006) and stimulus duration[5] (Zago et al., 2005). While the fact that seemingly minor changes in the experimental design can drastically affect the observed results is not news in the field of neuroscience, it serves as an important reminder for researchers to pay close attention to these minutiae when meta-analyzing other studies and designing their own.

So far we have been discussing the studies of practiced naming in which the tasks used in the encoding phase and in the testing phase were identical (picture naming in both cases). However, for patient treatment it is of particular importance that the effects of practice on a certain task in the speech pathologist's office generalize to other contexts in everyday life. To understand what normal mechanisms support such "transferable" effects of priming, a series of studies led by David Copland explored the effects of naming facilitation in healthy older adults. The three studies used the same pictorial materials at test and followed the same scanning protocols, thus providing optimal conditions for across-task comparisons. However, they employed different encoding tasks. The first study (Heath et al., 2012a) facilitated naming with a semantic decision task, in which subjects were required to answer questions about a visually presented stimulus, such as "Does it bark?" or "Does it live in the ocean?". In the second study (Heath et al., 2012b), naming was primed by auditory repetition with the concomitant picture presentation. Finally, the study by MacDonald et al. (2015), as discussed above, in the encoding phase used a picture naming task identical to the one used at test.

Somewhat surprisingly, in the two studies of priming that employed a different encoding task (Heath et al., 2012a, 2012b), activation in the inferior temporal cortex was not modulated by practice over the long term, despite the fact that facilitation sessions were conducted with the same pictorial stimuli used in MacDonald et al. (2015). This seems to contradict the view, presented earlier, that repetition suppression in this area reflects facilitated object recognition. While traditionally implicated in the processing of visual stimuli, the inferior temporal and fusiform gyri were shown to be sensitive to priming when both prime and

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[5] Whereas in most previous studies of object priming stimuli were presented for brief periods of time (200 ms in case of van Turennout et al., 2000, 2003 and Meister et al., 2005) and at rapid presentation rates (1.5-3.5 s per trial), MacDonald and colleagues opted for a stimulus duration of 3 s and overall longer trials (14.7 s).

target were presented auditorily (e.g., see word stem completion study by Buckner et al., 2000). More interestingly, occipitotemporal cortices were proven sensitive to the modality coherence of prime and target. For example, Badgaiyan et al. (1999) found no repetition suppression in these areas in cross-modal priming of word stems (from visual to auditory modality), and Schacter et al. (1999) reported for the same task that the magnitude of suppression was greater for within-modality than across-modality priming. Recently, Horner and Henson (2011) observed repetition suppression in occipitotemporal areas during a semantic (size classification) task, in which primes were presented as written words and targets were pictorial. Taken together, the findings of these studies suggest that the observed BOLD reductions in the inferior temporal areas do not reflect facilitation stemming merely from repeated presentation of the same visual stimulus, but rather could be modulated in a top-down fashion (Buckner et al., 2000)[6] or reflect the strengthening of stimulus-response associations (Horner & Henson, 2011)[7].

Interestingly, long-term practice both on auditory repetition (Heath et al., 2012b) and on a semantic task (Heath et al., 2012a) was accompanied by repetition suppression in the left middle temporal gyrus, an area associated with lexical-semantic processing. This suggests that the left IFG could be not the only region in the language network that is modulated by priming.

2.4. Disentangling task and item practice effects. From incidental practice to intensive training

The potential confounding of the results of the studies on practiced naming by task habituation was identified by Meltzer et al. (2009), whose primary goal was to evaluate the reliability of multisession training studies with aphasic patients. The longitudinal experiment, conducted on healthy young adults, involved naming of novel, repeated (presented in each scanning session) and "overlearned" (named once outside of the scanner immediately before

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[6] For a discussion on the role of top-down effects in priming refer to the seminal paper by Karl Friston introducing the predictive coding theory (2005); for a recent review, see (Auksztulewicz & Friston, (2016).

[7] Accounts of stimulus-response associations in priming can be found in Dobbins et al. (2004), Race et al. (2009), Horner & Henson (2008); for review, see Henson et al. (2014).

a session) objects in four fMRI sessions spaced one month away from each other. The linear trend contrast revealed a gradual suppression of activity in the left IFG and the insula for items in the repeated condition, consistent with the previous reports of naming priming[8]. Repeated naming of “overlearned” objects was associated with decreased activity in the left precentral gyrus, but not in the left IFG, which, according to the authors, could be explained by the fact that the lexical selection demands were minimized by explicit training prior to scanning and remained reduced throughout the testing. Finally, for both novel and repeated stimuli the magnitude of BOLD activation gradually declined across sessions in a number of areas, including the bilateral motor and inferior parietal cortices, as well as the supplementary motor area and the left premotor cortex. This finding points to the presence of previously unreported effects of task accommodation (since the changes were also observed for novel items introduced into each session, which could not be explained by priming). As suggested by Meltzer and colleagues (2009), neural changes that could result from habituation to the task, as opposed to practice on particular items, should be explicitly accounted for in studies of naming practice.

The possible contamination of word practice effects by task accommodation was taken into consideration by Basso and colleagues (2013) who looked into the effects of explicit naming practice in healthy young adults. In contrast to the previous studies, they adopted a paradigm of intensive training in which subjects underwent ten consecutive days of object naming practice. A training session consisted in naming twenty color photographs, ten times on each day. In order to tap into the abstract, structural object representations, each day participants received a new booklet depicting different exemplars of the same twenty objects. Two identical fMRI sessions were carried out — one before and one after the training protocol — in which the participants were asked to name the objects from black-and-white line drawings. In addition to twenty low-frequency words subjected to training, an equal number of untrained low-frequency items (serving as controls for potential task habituation effects) and

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[8] Note, however, that the direction of practice-related changes in the insula was different from that reported by van Turennout et al. (2000, 2003).

untrained high-frequency items (used to explore the effects of word frequency/familiarity and to compare them with the training effects) were included in the two fMRI sessions.

Across-session comparison of items belonging to all three experimental subsets (low-frequency untrained, low-frequency trained and high-frequency untrained) revealed similar BOLD decreases in the precentral and superior temporal gyri, as well as in the left middle occipital gyrus. These deactivations were attributed by the authors to task practice effects. However, it should be noted that, unlike Meltzer et al. (2009), the present study did not include novel items in the second fMRI session, but rather evaluated the effects of task practice by comparing the responses to the same items presented in the two experimental sessions. Thus, "task practice" in the sense of Basso et al. could encompass both the effects stemming from repeated performance on the same task in the same environment ("task habituation" in Meltzer et al.'s terminology) and those associated with repeated exposure to the same stimuli twice over the period of two weeks ("long-term priming" discussed in Sections 2.2–2.3). Indeed, as Basso et al. acknowledge, the observed deactivations were likely to stem from priming of visual object representations (extrastriate cortex), along with facilitation of articulatory planning (precentral gyrus) and phonological lexical retrieval (superior temporal gyrus) of the previously presented items.

More importantly for the aims of Basso et al.'s study, the visual comparison of session effects observed for trained and untrained items allowed to disentangle the effects of incidental practice (as identified by the across-session comparison of untrained items) and explicit, intensive practice (as identified by comparing trained items in the second vs. the first fMRI session). Namely, BOLD decreases in the left extrastriate cortex, that were observed for all experimental items, in the trained condition extended more rostrally and involved the posterior fusiform gyrus (BA 37), suggesting that explicit practice led to the strengthening of object representations at an exemplar-independent, abstract level. A second way of assessing the training-induced changes consisted in comparing activations to trained and untrained items in the second experimental session. This contrast revealed post-training activation increases in two bilateral clusters of the medial parietal cortex — namely, the central portion of the precuneus and the posterior cingulate gyrus — the structurally and functionally connected areas, speculated to be part of a neural network mediating the recollection of episodic knowledge (Yonelinas et al., 2005). Additional evidence came from the comparison of low-frequency and high-frequency nouns: whereas in the first fMRI session both low-frequency subsets yielded greater activations in the bilateral insula/IFG and in the anterior cingulate cortex as compared to the high-frequency items, in the second session this distinction was detectable for the "untrained low-frequency vs. high-frequency", but disappeared for the "trained low-frequency vs. high-frequency" contrast. The above described deactivations were similar to those reported by Meltzer et al. (2009) for repeated as opposed to novel items, suggesting that frequency and practice effects may have some common underlying mechanisms.

2.5. Naming practice of nouns and verbs

The majority of naming studies so far have focused on naming of common objects, referred to by nouns, and significantly less attention has been attributed to other word classes. It is understandable, considering that the world we live in is populated by objects, and that concrete objects are the easiest to depict on static images that are commonly employed as stimuli in naming tasks.

However, our ability to refer to operations performed on objects is no less crucial for normal communication than the ability to name the objects themselves. In language, these operations are typically conveyed by verbs. Verbs are very rich both semantically and grammatically. Not only do they describe the action/event/process itself, they also encode the information about its participants through the argument structure and provide the time frame in which it unfolds by means of tense and aspect.

Reports of selective word class deficits in neurological patients suggest that noun and verb processing is mediated by at least partially distinct neural networks (e.g., Miceli et al., 1984, 1988; Bastiaanse & Jonkers, 1998; for review, see Mätzig et al., 2009). According to one influential hypothesis, noun processing is subserved by middle and inferior temporal regions, whereas verb retrieval relies on the inferior frontal cortex (Damasio & Tranel, 1993). While this claim received supporting evidence from several studies in aphasic patients (for review, see Cappa & Perani, 2003) and, more recently, from the study of direct electrical stimulation during cortical mapping (Havas et al., 2015), its validity has been challenged by reports of prefrontal patients with spared verb retrieval (De Renzi & Di Pellegrino, 1995), as well as brain-lesioned patients with intact frontal lobes who showed impaired verb processing (e.g., Aggujaro et al., 2006; Silveri et al., 2003).

Whatever its locus, verb processing seems to be more demanding than noun processing, as evidenced by various sources. According to the anatomoclinical review by Mätzig et al. (2009), verb, as compared to noun, deficits are more prevalent in aphasia. Language acquisition studies commonly report noun bias in typically developing children and verb deficits in developmental disorders (Marshall, 2003). Finally, studies with healthy monolingual adults also suggest that verbs are inherently more complex. Behaviorally, this complexity manifests as longer naming latencies (Vigliocco et al., 2004; Kurland et al., 2018). Neuroimaging studies directly comparing the words of two classes consistently report that the “verbs > nouns” contrast yields activations in a number of brain areas, including the lateral temporal and inferior frontal cortices, while the opposite contrast (“nouns > verbs”) often fails to find any significant noun-specific signal increase (for reviews, see Crepaldi et al., 2011; Vigliocco et al., 2011). However, there is no agreement regarding the underlying nature of these distinctions. While some researchers proposed that grammatical class may represent the organizational principle of lexical knowledge in the brain (Caramazza & Hillis, 1991), others have pointed out that the root cause of the observed differences may lie in the separable conceptual representations of objects and actions, with additional differences arising at the level of morphosyntax (Vigliocco et al., 2011). Yet, as argued by Black & Chiat (2003), the two word classes differ simultaneously along multiple linguistic dimensions (at least, in English), including semantic, syntactic, morphological and phonological, each of which contributes to the overall greater verb complexity. Importantly, the comparison of nouns and verbs may be further complicated by additional confounding factors. One such potential confound is imageability — verbs are inherently less imageable than nouns, which can account for the additional resources attributed to their processing (Bird et al., 2000, 2003).

Regardless of the causes of the observed distinctions, it seems plausible that the two word classes could be differently modulated by naming practice. In a recent study, de Aguiar and colleagues (in preparation) replicated Basso et al.'s (2013) training paradigm in the context of an action naming task. As in the original study, they trained healthy young speakers of Italian for ten consecutive days and scanned them on the days preceding and following the training; during the training and in the two experimental sessions participants were instructed to name actions using verbs in the infinitive form. Similarly to practice with nouns (Basso et al., 2013; Meltzer et al., 2009), verb training was associated with decreased activity in the left IFG/insula. At the same time, two right-hemispheric clusters revealed post-training activation increases — one in the middle temporal gyrus/inferior temporal sulcus, potentially reflecting facilitated lexical-semantic processing (Hickok & Poeppel, 2007), and another one in the posterior parietal lobe, implicated in processing of motor and spatial action representations (Andersen et al., 1997). Task practice effects, assessed by contrasting the untrained items in the second vs. the first fMRI session, consisted of increased activation in the posterior cingulate cortex (PCC) and the precuneus bilaterally, as well as in the right superior parietal lobe. While the authors attributed inactivation of the medial parietal structures to recruitment of episodic memory, this explanation seems unlikely, considering that a similar (or greater) inactivation would be expected for trained items, which was not the case. These findings are also at variance with the results obtained by Basso et al. (2013), who reported similar increases for trained, but not for untrained words. However, the results of the two studies cannot be compared directly, due to the differences in statistical power and statistical thresholding methods.

The potential interaction between training and word class effects was addressed by Kurland et al. (2018), who combined nouns and verbs in one paradigm. Healthy 48-76 year old participants, native speakers of English, participated in the experiment. Testing was conducted in two identical fMRI sessions, spaced by approximately one month. Despite the superficial similarity to Basso et al.'s training paradigm, no actual training took place between sessions. Instead, practiced items were facilitated via a repetition paradigm, once at a long delay (on one of the days preceding fMRI1; five repetitions in total) and once immediately prior to both fMRI1 and fMRI2 (five repetitions before each session). Stimuli were repeated twice during a session, which allowed to additionally assess the effects of short-term priming. Naming latencies collected during task performance in the scanner revealed significant main effects of practice ($RT_{PRACTICED} < RT_{UNPRACTICED}$), repetition ($RT_{RUN2} < RT_{RUN1}$) and word class ($RT_{NOUNS} < RT_{VERBS}$), as well as a significant interaction of practice and repetition. More interestingly, a significant interaction of practice and word class was documented, suggesting that action naming was facilitated by practice to a greater degree than object naming. The fMRI results confirmed the presence of significant main effects of word class and practice, but did not corroborate the behavioral evidence of the practice by word class interaction. A significant main effect of word class was found in a number of regions that yielded greater response to verbs than to nouns, including the middle temporal gyrus bilaterally, left middle occipital gyrus and right fusiform. A significant main effect of practice was observed in the bilateral precuneus and left inferior parietal lobule (IPL), and, at a more liberal threshold ($p < .001$, uncorrected), in the homologous right IPL and right PCC — all these areas showed increased BOLD response after practice. The practice-related inactivations were very similar to those reported by previous studies of repeated naming (MacDonald et al., 2015, Basso et al., 2013). The angular gyrus, in concert with medial parietal areas, is implicated in recollection from episodic memory (Thakral et al., 2017), supporting the interpretation of the parietal BOLD increases in terms of long-term memory engagement.

An additional across-session comparison showed a greater BOLD response in the right parahippocampal cortex to practiced items in fMRI1 as compared to fMRI2. The decay of hippocampal activity has previously been reported during training of novel vocabulary (Breitenstein et al., 2005; Davis et al., 2008). However, the interpretation of Kurland et al.' findings is complicated by the fact that the effects of long-term and short-term practice are systematically confounded, since the same items are facilitated at both lags. Thus, it is not clear whether long-term or short-term facilitation contributed to the BOLD effects: on the one hand, hippocampal activity could have decreased as a result of additional practice immediately prior to fMRI2; on the other, it could have stemmed from delayed consolidation.

A complementary ROI analysis targeted the regions selected by MacDonald et al. (2015) and an additional region in the posterior middle temporal gyrus (based on the report by Fridriksson, 2010), as well as their right-hemisphere homologues (i.e., 16 ROIs in total). Following the FDR correction for multiple comparisons (Benjamini & Hochberg, 1995), a significant main effect of practice was found in the left pars opercularis and pars orbitalis, as well as the left inferior temporal gyrus — all three ROIs revealed repetition suppression following practice. No significant interactions were found in any of the regions, thus, again failing to corroborate the observed behavioral effects of modulation of practice effects by word class. A main effect of word class was observed in the middle and inferior temporal gyri bilaterally, in line with the proposed role of these regions in action processing (Lingnau & Downing, 2015), in bilateral extrastriate cortices (possibly due to the lack of proper stimulus matching for visual complexity), as well as in the right posterior superior temporal gyrus and the left pars opercularis. Interestingly, both the effect of session and that of repetition (within a run) had opposite directions in different regions, suggesting that both repetition suppression and repetition enhancement could arise as a result of short-term and long-term priming. Unfortunately, a univocal interpretation of these results is, as already mentioned above, complicated by the fact that the same stimuli were facilitated both over a short and a long term.

In summary, the studies of noun and verb naming practice provide inconsistent results. So far, only one study (Kurland et al., 2018) has attempted to directly compare naming practice of nouns and verbs. In this study, however, the practice by word class interaction observed at the behavioral level was not supported by neuroimaging data. One potential reason for this outcome is that practice was not intensive enough as to yield significant BOLD changes. Thus, potential content-specific effects of naming practice remain to be addressed.

3. Discussion

Picture naming is a complex process, involving multiple stages on the way from the initial perceptual processing of a visual stimulus to the articulation of a word response (Indefrey & Levelt, 2004). Practice on this task can, in theory, affect brain regions mediating any of these stages (Francis, 2014). At the same time, areas that are not initially involved in task performance may become engaged after practice, which can be explained by novel network formation or the involvement of episodic memory (for review, see Segaert et al., 2013). Below we will briefly summarize the key findings of the reviewed studies regarding the neural underpinnings of picture naming practice.

3.1. Object recognition and occipitotemporal regions

The commonly reported repetition suppression in occipitotemporal areas most likely stems from the facilitation of object recognition. While priming is undetectable in early visual areas (V1, V2), it affects regions located higher up in the ventral visual stream, from the bilateral extrastriate cortices to the fusiform. The extrastriate decreases following picture priming are immediate (van Turennout et al., 2000, 2003) and can be maintained for more than a week (Basso et al., 2013). They likely reflect facilitated processing of low-level visual features, such as shape (Malach et al., 1995), considering that they are observed both for real and nonsense objects (van Turennout et al., 2000). Deactivation in the fusiform is long-lasting and was reported to persist for more than a month following a brief stimulus exposure (Meister et al., 2005). Interestingly, the fusiform reveals exemplar-general priming, as shown by Basso et al. (2013) who found repetition suppression in this area after training on images that differed from the drawings used during the testing sessions. This speaks in favour of the abstract nature of representations stored in this area. However, the fact that fusiform deactivation is often missing when the tasks used for encoding and for testing differ suggests that suppression in this area may reflect stimulus-response binding (Henson et al., 2014), in addition to facilitation of perceptual/conceptual stimulus processing.

3.2 Word production processes and left frontal cortex

At the same time, anterior brain regions show practice-related changes, in all likelihood reflecting facilitation of word processing. Deactivation in the left IFG is most consistently reported across the studies of incidental and explicit naming practice. However, the interpretation of this suppression is complicated by the lack of consensus on the functional parcellation of the left IFG with regards to language (e.g., see contradictory views on the function of BA45 in Poldrack et al., 1999 vs. Vigneau et al., 2006), which makes "reverse inferences" (Poldrack, 2006) on the nature of facilitated processes unreliable. The problem is aggravated by the large intersubject variability in cytoarchitecture of the so-called "Broca's area" and its poor mapping to macroanatomical landmarks (Amunts et al., 1999), rendering the commonly used labelling of activations in terms of Brodmann areas virtually useless.

Repetition suppression in the left IFG was also interpreted in terms of domain-general, executive functions, such as selection and inhibition of competing responses (Thompson-Schill et al., 1999). Another account suggests that reduced response in this area following practice could stem from stimulus-response mapping (Race et al., 2009; MacDonald et al., 2015). According to a recent report by Fedorenko et al. (2012), subregions of Broca's area mediating language-specific and domain-general functions are interwoven, suggesting that techniques with relatively poor spatial resolution such as fMRI may fail to distinguish between them. Future research on the functional parcellation of the left IFG will help shed light onto the underlying nature of repetition suppression observed in this region.

The adjacent left insular cortex was also reported to show practice-related activation changes. Whereas the early studies of language practice reported increased BOLD activity in this area simultaneously with declining activity in the left IFG (Raichle et al., 1994; van Turennout et al., 2000, 2003), later studies found a concurrent deactivation of both regions as a function of practice (Meltzer et al., 2009; Basso et al., 2013; de Aguiar et al., in preparation). At this stage, no clear explanation can be given to the discrepancy in the observed results. In a different cognitive domain, Henson (2016) uses the example of face priming in the fusiform to show that activity in the same region can be either suppressed or enhanced based on a variety of factors, including attentional demands of a task and stimulus novelty, among others. By analogy, specific task/stimulus characteristics might be accountable for the contrasting direction of the changes in the insular cortex.

3.3. Explicit memory and parietal areas

Finally, several regions in the parietal cortex — including the bilateral precuneus and the PCC on its medial surface, and the left IPL on its lateral surface — display increased response to practiced items. Early studies of primed naming (van Turennout et al., 2000, 2003; Meister et al., 2005) could not detect practice-related changes in these areas due to the fact that they masked their analyses to the areas initially involved in picture naming. The significant increase of the BOLD amplitude in the mesial parietal cortex can be observed already after a few repetitions (Kurland et al., 2018; MacDonald et al., 2015), and is significantly stronger for intensively trained items than for those that were presented only twice (Basso et al., 2013; but see de Aguiar et al., in preparation). Sensitivity of these areas to practice has also been demonstrated in the context of repeated sentence processing in healthy subjects (Hasson et al., 2006; Poppenk et al., 2016). Additionally, there is evidence that there areas are modulated by incidental naming practice (Heath et al., 2015) and intensive naming therapy (Fridriksson, 2010) in anomic patients. The precuneus, PCC and IPL are all associated with retrieval of knowledge from episodic (Yonelinas et al., 2005; Seghier, 2013), and potentially even semantic memory (Binder et al., 2009; Fairhall & Caramazza, 2013). Their structural and functional connections to the language network remain to be explored.

Chapter 3. Practiced naming of objects and actions in healthy monolingual adults: An fMRI study

1. Introduction

As discussed in Chapter 2, little research so far has been devoted to the investigation of the neural correlates of intensive naming practice in healthy monolingual individuals. While training words that already exist in the lexicon might seem like an exotic task, previous studies on practiced naming of low-frequency nouns (Basso et al., 2013; Kurland et al., 2018) and verbs (de Aguiar et al., in preparation; Kurland et al., 2018) showed that healthy subjects significantly improve on a naming task following training, as evidenced by shorter response latencies and BOLD activation changes in a number of brain areas, both within and outside the language network.

Importantly, findings of these studies not only contribute to our understanding of the neural mechanisms supporting practice in the healthy brain, but could also potentially assist in the interpretation of training studies conducted with patients suffering from aphasia. An increasing number of neuroimaging studies focus on functional plasticity that takes place in anomic speakers undergoing therapy for naming disorders (e.g., Fridriksson et al., 2006, 2007; Meinzer et al., 2006; Vitali et al., 2007). These studies seek to unravel a potential interaction between brain activation changes associated with naming practice and the magnitude of improvement, in an attempt to determine the neural loci that could serve as predictors of treatment outcome. Although the therapy-induced plasticity may vary substantially depending on a variety of factors pertaining to lesion and patient characteristics, recent evidence suggests that, at least for some individuals with aphasia, practice-related naming facilitation may partially rely on the same mechanisms that are engaged in healthy controls (Heath et al., 2015).

In order to investigate these mechanisms, we conducted a ten-day “simulation” of naming treatment with neurologically intact speakers of Italian, following a training paradigm outlined by Basso and colleagues (2013). In order to extend on Basso et al.’s findings, we included into the training set both low-frequency nouns and low-frequency verbs. The use of two experimental sessions (pre- and post-training) allowed us to examine the object and action naming networks prior to training and to investigate the changes observed in (and outside of) such networks as a result of practice.

The experiment was conducted with two separate groups of subjects. The first group participated in a strictly behavioral protocol. The other group followed the same training protocol, but completed the two experimental sessions, before and after training, in the scanner. In addition to the conventional GLM analyses of the fMRI data, we have tested the performance of the searchlight pattern classification analysis, recently introduced in the neuroimaging community (Kriegeskorte et al., 2006).

2. Materials and methods

2.1. Participants

Thirty-five native Italian speakers took part in this project — 12 individuals (3 male, mean age: 23.3 ± 2.5 years, age range: 19-28 years) were recruited for the behavioral study, and 23 volunteers (9 male, mean age: 23.7 ± 3.3 years, age range: 19-32 years) participated in the fMRI study. Three participants in the fMRI study were subsequently excluded from the data analyses — two due to excessive head motion during scanning (more than 3 mm in one of the directions), and one due to non-compliance with the training protocol. All but one of the participants were deemed right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971); the remaining subject was a self-reported right hander, but scored as ambidextrous on the Inventory. All participants had normal or corrected-to-normal vision and no reported history of neurological or psychiatric disease.

The study was conducted in compliance with the Declaration of Helsinki and was approved by the Human Research Ethics Committee of the University of Trento. All participants signed informed consent forms.

2.2. Stimuli

2.2.1. Preliminary naming task

First, we conducted a preliminary naming task with each subject. The goal of the preliminary testing was to assure that participants could recognize objects and actions from the pictorial stimuli and could retrieve their corresponding names. Stimuli included line drawings of 80 objects and 80 actions that were presented to subjects at a comfortable pace using a PowerPoint presentation. Subjects were instructed to produce names of objects using an Italian noun in a singular form (without an article) and to produce names of actions using a verb in the infinitive form. Part of the pictorial stimuli were specifically drawn for the present study, while others were selected from various sources, including the Verb and Action Test (VAT; Bastiaanse et al., 2016), the Battery for the Analysis for the Aphasic Deficit (BADA; Miceli et al., 1994), as well as the public domain. If a word produced by a subject deviated from the dominant response[9], the experimenter corrected the subject immediately, and asked to repeat the target names of all deviating responses in the end of the session.

2.2.2. Experimental naming task

Out of the 160 drawings delivered to participants in the preliminary naming task, 40 object and 40 action pictures were selected to be used in the two identical experimental naming sessions. Half of the items in each set were included in the training protocol, while the other half were not explicitly trained between the experimental sessions, and served as controls for potential stimulus priming/task habituation effects. The four resulting subsets — untrained nouns (NU; n = 20), trained nouns (NT; n = 20), untrained verbs (VU; n = 20) and trained verbs (VT; n = 20) — were matched for a number of variables previously reported to affect word retrieval. Namely, words in the four subsets were balanced for phonemic ($\chi_2(3) = .43$, $p = .934$) and syllabic ($\chi_2(3) = .804$, $p = .848$) length, as well as for relative lemma frequency ($\chi_2(3) = .006$, $p = .996$), as indicated in the lexical database of written Italian (Corpus e Lessico di Frequenza dell'Italiano Scritto, CoLFIS;

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[9] The dominant response for pictures used in the experiment was identified in the course of an online naming agreement survey conducted with a separate group of subjects; for more details, see Section 2.2.2.

Bertinetto et al., 2005). Online questionnaires, created on the website SurveyMonkey.com, were delivered to separate groups of Italian native speakers in order to balance target words for familiarity (60 participants; $\chi^2(3) = 2.629$, $p = .452$), imageability (38 participants; $\chi^2(3) = 6.549$, $p = .088$)[10] and subjective age of acquisition (55 participants; $\chi^2(3) = 3.473$, $p = .324$). Another questionnaire was used to balance naming agreement of pictorial stimuli (48 participants; $\chi^2(3) = 2.158$, $p = .54$). Additionally, we matched the pictures for objective visual complexity ($\chi^2(3) = .245$, $p = .97$) using the GIF lossless compression method (Forsythe et al., 2008).

Nouns were selected from a broad range of semantic categories, including animals, professions, clothing, furniture, buildings, vehicles, fruit and vegetables. While a number of previous studies investigating neural representations of objects focused on tools (for review, see Martin, 2007), we deliberately avoided the use of tools in our stimulus set, since they are conceptually related to actions and are believed to share neural correlates with verbs (for review, see Lewis, 2006). Verbs were additionally roughly matched for transitivity and instrumentality. For full list of stimuli, see Appendix A.

Pictures were normalized with an average brightness of 128 cd/m^2. Fourier-transformed phase-scrambled images were additionally introduced into the experimental set in order to control for visual and articulatory processing. In the second experimental session all images were flipped horizontally in order to reduce potential effects of low-level priming in early visual areas.

2.2.3. Training materials

During training, subjects were asked to practice overt naming of 20 objects belonging to the NT subset and 20 actions from the VT subset. For this purpose, we compiled ten booklets with color photographs — one for each day of training. Photographs were taken from the public domain and represented different exemplars of to-be-trained objects and actions, so that each training day a subject saw a new picture of the same object/action. Each booklet was divided into two sections — "Objects" and "Actions"; order of item presentation within each section was randomized.

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[10] The effect of imageability showed a subtle trend towards statistical significance ($p < .088$). However, this is the most optimal matching we could achieve, considering that verbs are inherently less imageable than nouns (Bird et al., 2003).

2.3. Procedure

The experimental paradigm is schematically depicted in Fig. 3.1. Subjects underwent intensive naming training for ten consecutive days (excluding weekends). Training material comprised 20 objects (the NT subset) and 20 actions (the VT subset). Training was carried out at home, at a time comfortable for a subject. In order to test if participants complied with the training protocol, they were asked to record their responses with the help of a digital recorder. A daily training session consisted in naming all items in an action booklet and in an object booklet for a total of ten times.

All participants completed two identical experimental sessions — one before and one after the training. Some subjects underwent the picture naming task outside of the scanner, while their response times (RTs) were measured (Section 2.3.1), while others followed an analogous procedure in the MRI scanner (Section 2.3.2). Along with the 40 objects and actions involved in training (the NT and VT subsets), participants were presented with an equal number of untrained items (the NU and VU subsets). The task was to overtly name the depicted object or action using a single Italian word (a noun without an article or a verb in the infinitive form). When presented with scrambled images, subjects were instructed to produce a pseudoword — */ber:'tova/* (in session 1) or */sin:'toti/* (in session 2).

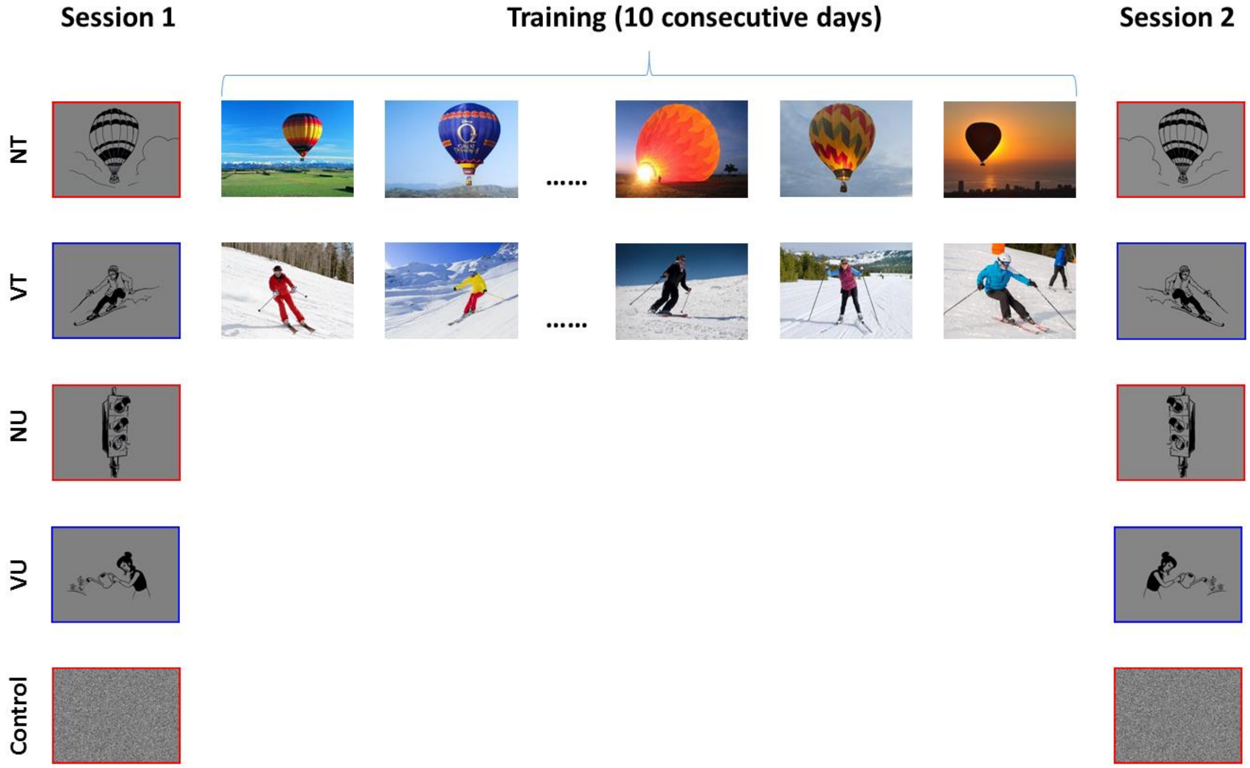

Figure 3.1: The experimental paradigm. Participants trained naming of 20 objects (NT) and 20 actions (VT) at home for ten consecutive days using color photographs. Before and after the training, they underwent two identical experimental naming sessions that, along with the trained items, included 20 untrained objects (NU) and 20 untrained actions (VU) that were used as controls for potential task habituation effects. Fourier-transformed phase-scrambled images (Control), in response to which subjects were instructed to produce a previously learned pseudoword, were additionally included into the stimulus set to control for low-level visual processing and articulation.

Stimuli were presented in a blocked design. A run consisted of four blocks — NU, NT, VU and VT — presented in random order. Each block included five items belonging to one of the four experimental conditions, as well as two scrambled images randomly interspersed into a block. Word class was cued by a frame that appeared around an image: red frame for nouns in the NU and NT blocks, blue frame for verbs in the VU and VT blocks. Frames were also placed around scrambled images; the color depended on the type of the block a scramble appeared in and was not meaningful — subjects were instructed to produce the same pseudoword irrespective of frame color. All stimulus items (n = 80) were presented within four experimental runs, and subsequently repeated within four additional runs in a different order[11].

Prior to each experimental session, participants received written instructions and underwent short practice.

Stimulus presentation and response collection were controlled with ASF software (Schwarzbach, 2011) based on the Psychtoolbox-3 (Brainard, 1997) for MATLAB (The Mathworks, Inc., Natick, MA, United States).

2.3.1 Behavioral naming task

The first experimental session took place on the day after the delivery of the preliminary naming task. Training started between 1 to 3 days after the first experimental session (mean: 1.9 days) and finished on the day preceding the second experimental session. Subjects were allowed to take 1-3 days of rest from training during weekends (mean: 2 days).

Each trial started with a 2 s black fixation cross followed by a 3 s picture presentation. The duration of inter-trial interval was set to 1 s. Blanks with a duration of 5 s were introduced between the blocks, as well as at the beginning and at the end of each run. Subjects were instructed to reply as soon as they saw a picture on the screen.

Stimuli were presented on an LCD screen with the resolution of 1920 × 1080 pixels and the frame rate of 60 Hz.

2.3.2 fMRI naming task

The preliminary naming task was administered 1 to 4 days prior to the first fMRI session (mean interval: 1.5 days). The training procedure started 1 to 4 days after the first fMRI session (mean:

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[11] Due to technical reasons, for one of the participants of the fMRI experiment only four runs out of eight in the first experimental session could be acquired.

1.9 days) and finished on the day preceding the second fMRI session. Subjects were allowed to take 1-4 days of rest from training (mean: 2.2 days).

Each trial started with a black fixation cross whose presentation lasted between 2 and 5 s. The duration of the initial fixation was chosen from a geometric distribution ($p = .4$; in steps of 1 s). The fixation cross was followed by a 2 s picture presentation. Unlike in the behavioral experiment, in the fMRI setting subjects were instructed to withhold their overt responses while they viewed the picture. Instead, they were asked to respond when they saw a green fixation cross (3.5 s) that followed a picture. Trial structure is schematically depicted in Fig. 3.2. The inter-trial interval was jittered between 0.5 and 1 s (in steps of 0.25 s). Blanks with a duration of 6 s were introduced between blocks. Each run started and ended with a 12 s blank.

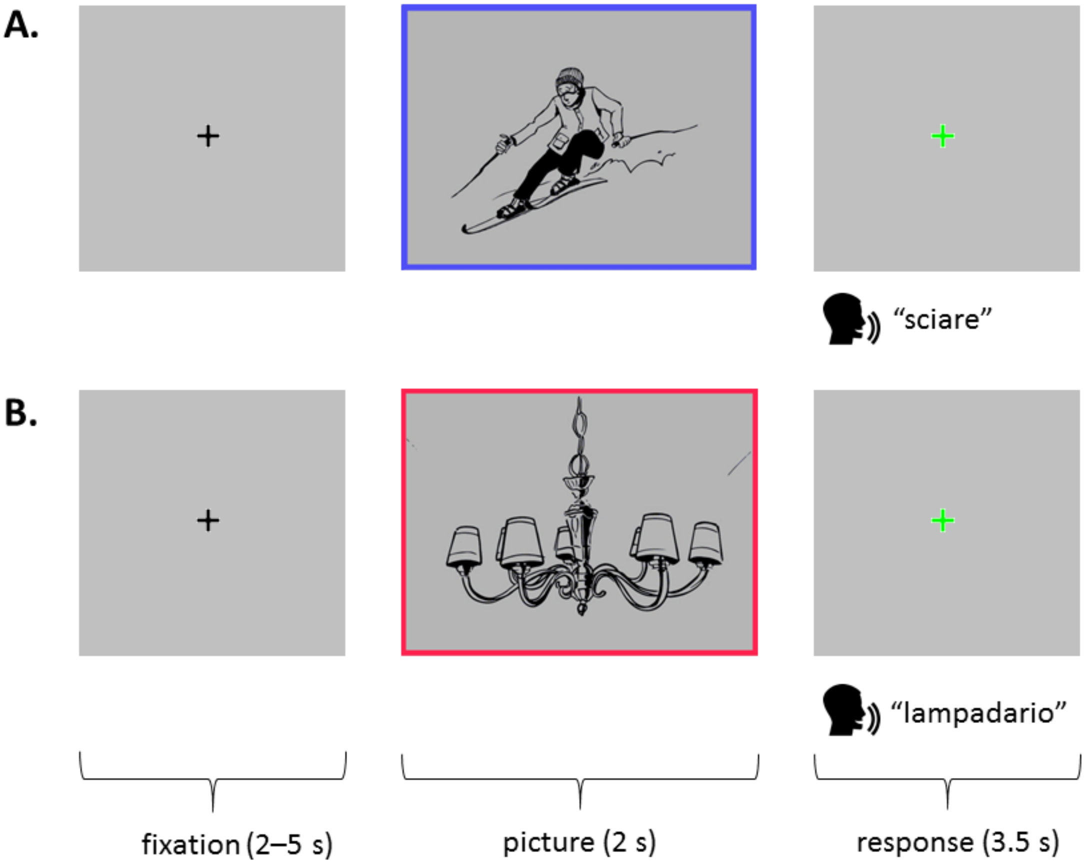

Figure 3.2: fMRI trial structure. a. Example of an action trial (subsets VU and VT; blue frame), *'to ski'*. b. Example of an object trial (subsets NU and NT; red frame), *'chandelier'*. Response was cued by a green cross.

In the scanner, stimuli were back-projected onto a screen (frame rate: 60 Hz, screen resolution: 1024 × 768 pixels) via a liquid crystal projector (OC EMP 7900, Epson, Nagano, Japan). Participants viewed the screen binocularly through a mirror mounted on the head coil.

2.4. Data acquisition

2.4.1. Behavioral data acquisition

Vocal responses were collected using the Samson Q4 microphone with a low-noise microphone cable (Thomann, UK). RTs were measured automatically using the voice key function supplied with ASF. Recordings were digitized at a sampling rate of 44.1 kHz.

2.4.2. Neuroimaging data acquisition

MR data were collected at the Functional Neuroimaging Laboratories of the University of Trento (LNiF, Mattarello) using a 4 Tesla Bruker MedSpec scanner (Bruker BioSpin MRI GmbH, Ettlingen, Germany) with an 8-channel birdcage head coil. Functional images were acquired using a T2*-weighted gradient echo-planar imaging (EPI) sequence with fat suppression. Scanning was performed continuously during a functional run with the following parameters: repetition time (TR) = 2.2 s, echo time (TE) = 33 ms, flip angle (FA) = 75°, field of view (FOV) = 192 × 192 mm, matrix size = 64 × 64, voxel resolution = 3 × 3 × 3 mm. We acquired 31 slices in ascending-interleaved odd-even order, with a thickness of 3 mm and a 15% gap (0.45 mm). Slices were aligned with the AC-PC plane[12]. An imaging volume was positioned to cover the entire temporal lobe; as a result, a small portion of the superior parietal cortex was not captured in most subjects. The number of volumes in a functional run varied (range: 130-142) as a result of temporal jittering introduced into trials. Before each run we performed an additional scan measuring the point-spread function (PSF) of the acquired sequence, in order to correct the distortion in geometry and intensity expected with high-field imaging (Zaitsev et al., 2004; Zeng and Constable, 2002).

At the beginning of each scanning session, we performed a T1-weighted structural scan that served as reference for coregistration of functional data. Structural images were acquired using a magnetization-prepared rapid-acquisition gradient echo (MPRAGE) sequence (TR = 2.7 s, TE = 4.18 ms, FA = 7°, FOV = 256 × 224 mm, 176 slices, inversion time (TI) = 1020 ms), with

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[12] The AC-PC plane goes through the bicommissural line connecting the anterior commissure (AC) and the posterior commissure (PC).

generalized autocalibrating partially parallel acquisition (GRAPPA) with an acceleration factor of 2.

During a functional run, vocal responses were recorded using a fiber optic microphone (FOM1-MR, Fibersound, Micro Optics Technologies, Inc., Cross Plains, WI, United States).

2.5. Data processing and analyses

2.5.1. Behavioral data analysis

Voice onset intensity threshold was calibrated for each subject individually based on the visual inspection of wave plots of vocal responses with displayed RTs at a given threshold that were produced by the ASF software for each trial. RTs deviating from a subject's mean by more than two standard deviations were considered to be outliers and were removed from the analysis (5.2% of the data removed, including 3.4% of object trials, 9.9% of action trials and 1.4% of control trials that required the production of a pseudoword).

After the individual descriptive statistics were calculated in MATLAB R2015b, the data were submitted for inferential analysis with repeated-measures ANOVAs and paired-samples *t*-tests in SPSS 24.

2.5.2. fMRI data analysis

Neuroimaging data were preprocessed and analyzed using BrainVoyager QX 2.8.4 (Brain Innovation B.V., Maastricht, the Netherlands) in combination with the NeuroElf toolbox (v. 1.1; Weber, neuroelf.net) and in-house software written in MATLAB. The first three volumes of a functional run were discarded to avoid T1 saturation. For each run, we performed slice timing correction (cubic spline interpolation), followed by 3D motion correction (trilinear interpolation for estimation and sinc interpolation for resampling, all functional volumes acquired in a session realigned to the first volume of the first run) and temporal high-pass filtering with linear trend removal (cut-off frequency of 3 cycles per run). For the univariate analysis the functional data were additionally spatially smoothed with a Gaussian filter of 6 mm full-width half maximum

(FWHM) in order to reduce noise and minimize anatomical differences between subjects. Functional and structural data were aligned to each other in several steps, using the rigid-body transformation with 6 parameters (3 translations, 3 rotations). At a first step, the first volume of the first functional run in a session was coregistered to an anatomical image for the corresponding session. Next, anatomical scans obtained in the two sessions with a participant were aligned to each other. Finally, functional data from both sessions were coregistered to one of the anatomical images using the transformation parameters obtained during the intersession anatomical alignment. For the group analysis, structural and functional data were transformed into the Talairach stereotactic space (Talairach & Tournoux, 1988), using sinc interpolation.

2.5.2.1. Univariate analyses

Statistical analyses were performed with a general linear model (GLM), as implemented in BrainVoyager. A trial was modeled as an epoch lasting from the picture onset to its offset (2 s). Regressors included predictors of the 10 experimental conditions (2 sessions × 5 conditions: S1_NU, S1_NT, S1_VU, S1_VT, S1_Control, S2_NU, S2_NT, S2_VU, S2_VT, S2_Control). Additionally, 6 parameters resulting from head motion correction were included in the model as regressors of no-interest. Subject design matrices contained concatenated data from the two sessions (16 runs in total, 8 per session). Each predictor was convolved with a dual-gamma hemodynamic response function (HRF; Friston et al., 1998). The resulting reference time courses were used to fit the signal time courses in each voxel.

Since we were primarily interested in training effects and how they could potentially be modulated by word class, we restricted the volumetric ROI analysis (Section 2.5.2.1.1) to the data from the second, post-training session. Subsequently, we performed an exploratory whole-brain analysis on the surface, based on the data from both sessions (Section 2.5.2.1.2), in which we investigated training effects by contrasting trained and untrained items within and across sessions and looked for potential session effects stemming from task habituation/priming.

2.5.2.1.1. ROI selection and univariate ROI analysis

We selected 10 left-hemispheric ROIs defined as spheres with a 5 mm radius (Fig. 3.3) centered around the coordinates reported in previous studies. Coordinates given in the MNI convention were converted to the Talairach system using a tool supplied with the Yale BioImage Suite Package (Papademetris et al., http://www.bioimagesuite.org; Lacadie et al., 2008). Six ROIs targeted the areas associated with different stages of word production. Word production involves a large brain network and selecting a few coordinates out of the many reported in the relevant literature over the years is a non-trivial task. For the sake of consistency, we decided to investigate the same regions that were selected for analysis in a recent study on the effects of practiced naming in healthy older adults (MacDonald et al., 2015). These regions were chosen based on language-related meta-analyses (Vigneau et al., 2006; Indefrey & Levelt, 2004) and the authors' own previous work on practiced naming (Heath et al., 2012a, 2012b), and included three frontal ROIs within the left inferior frontal gyrus (IFG), including the pars orbitalis (-36, 27, -5), the pars triangularis (-41, 17, 6) and the pars opercularis (-52, 10, 20), and three temporal ROIs, comprising a posterior part of the superior temporal gyrus (postSTG; -48, -38, 14), a middle section of the middle temporal gyrus (midMTG; -55, -37, 5)[13] and a posterior portion of the inferior temporal gyrus (postITG; -44, -59, -7). Additionally, a region in the extrastriate cortex (-38, -82, -4) was chosen as an area consistently reported in the studies of object priming (for review, see Schacter & Buckner, 1998) and practiced naming (van Turennout et al., 2000, 2003; Meister et al., 2005; Basso et al., 2013), at both short (seconds and minutes) and long (days and weeks) repetition lags. The remaining three ROIs were centered around the cluster peaks reported in Basso et al. (2013). We hypothesized that intensively practicing an item (and, thus, artificially increasing its frequency), could result in activation changes associated with frequency effects. For this reason, we picked a region in the anterior cingulate cortex (ACC; -1.9, 14, 6.1) that showed significantly greater activation in response to high-frequency as compared to low-frequency nouns. We also selected two domain-general regions on the medial brain surface that

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[13] We will refer to this ROI as "midMTG" throughout the text. It should be noted, however, that its peak coordinate falls on the border between middle and posterior temporal regions that was delineated by Indefrey & Levelt (2004).

were associated in Basso et al.'s study with explicit item training, including the posterior cingulate cortex (PCC; -3.5, -36, 27) and the central portion of the precuneus (-4.4, -71, 31).

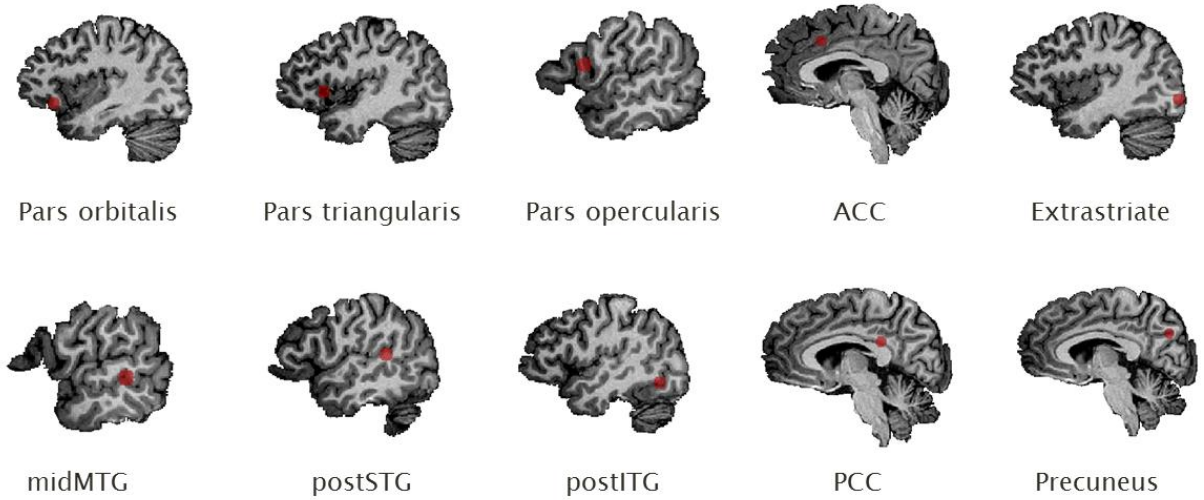

Figure 3.3: Ten spherical ROIs in the left hemisphere selected for analysis projected on the anatomy of a reference subject. ACC = anterior cingulate cortex, midMTG = mid-portion of middle temporal gyrus, postSTG = posterior superior temporal gyrus, postITG = posterior inferior temporal gyrus, PCC = posterior cingulate cortex

We extracted individual mean beta weights as an estimate of the BOLD amplitude for each condition of interest in the second session (NU, NT, VU, VT) from each ROI and submitted them to a two-way repeated-measures ANOVA with factors word class (nouns, verbs) and training (trained, untrained).

2.5.2.1.2. Univariate whole-brain analysis

For the whole-brain analyses, we moved from the brain volume to the cortical surface. The goal of this was twofold. First, restricting the analysis to the cortex helped us reduce the massive problem of multiple comparisons that all whole-brain studies suffer from (Lindquist & Mejia, 2015). Second, it allowed us to perform the cortex-based alignment (CBA). By taking into account the variability in gyral and sulcal folding patterns observed across participants, this procedure enables better intersubject alignment of structural and functional data. To this end, we segmented the white/grey matter border on individual Talairach-transformed T1-weighted anatomical scans and reconstructed 3D hemispheric meshes for each participant. Next, we performed the CBA procedure, as implemented in BrainVoyager. We inflated each mesh to a sphere with cortical curvature maps projected onto it (with four coarse-to-fine levels of smoothing) and aligned it to a standard spherical surface using a coarse-to-fine moving target approach (Fischl et al., 1999; Goebel et al., 2006). Transformation maps obtained as a result of this procedure were used to create two group-averaged surface meshes (for the left and the right hemisphere).

The statistical analyses were performed separately for each hemisphere. First, we created mesh time courses for each run by sampling the functional data from -1 to 2 mm from the reconstructed white/grey matter boundary. At the first level of statistical analysis, we ran individual fixed-effects (FFX) GLMs in subject space (i.e., prior to CBA) and obtained *t*-statistics for main effects of the experimental conditions. These *t*-maps were subsequently aligned to the group-averaged meshes using the aforementioned transformation matrices. At the group level, individual CBA-transformed *t*-maps were stacked together and submitted to the permutation analysis. Statistical maps for contrasts of interests were *z*-scored and corrected for multiple comparisons using Threshold-Free Cluster Enhancement (TFCE, Smith & Nichols, 2009), as implemented in the CoSMoMVPA toolbox (Oosterhof et al., 2016). A total of 1000 Monte Carlo simulations and a corrected cluster threshold of $p = .05$ (two-tailed; $z_{\text{min}} = -1.96$, $z_{\text{max}} = 1.96$) were used. Maps were projected onto the group-averaged hemispheric meshes for visualization.

The obtained activations were described using the surficial macroanatomical atlases supplied with BrainVoyager that were CBA-transformed and projected onto the group-averaged meshes.

2.5.2.2. Multivariate whole-brain analysis

In addition to the standard whole-brain GLM, we performed a multivariate pattern analysis (MVPA). This method, introduced by Haxby and colleagues (2001), is based on comparing spatial patterns of activation in response to different experimental conditions, as opposed to contrasting the magnitude of BOLD responses in individual voxels, as is the case in the framework of univariate analysis (for review, see Haxby, 2012).

We performed a whole-brain searchlight analysis (Kriegeskorte et al., 2006) on the brain surface (Oosterhof et al., 2011), using a linear discriminant analysis (LDA) classifier, as implemented in CoSMoMVPA.

The two decoding analyses aimed to test (1) in what areas the classifier can reliably (i.e., significantly above chance) distinguish between nouns and verbs (using the data from the first, pre-training, fMRI session), and (2) in which regions we would be able to decode trained and untrained items (based on the data from the second, post-training, fMRI session).

To this end, we ran single-study GLMs separately for each run with a subject, using design matrices created for the univariate analysis (Section 2.5.2.1) and unsmoothed mesh time courses created on a hemispheric surface of a subject (prior to CBA). At the single-subject level, maps containing *t*-statistics for main effects of experimental conditions for each run in a session were stacked together[14] and submitted to the searchlight analysis with an 8 mm radius. Classification accuracies were obtained using a leave-one-out cross-validation method with an 8-fold partitioning scheme: the dataset was split into 8 chunks (each corresponding to one experimental run) — the classifier was trained on the data from 7 chunks and tested on the remaining one. The procedure was repeated for 8 iterations, using all possible train/test partitions, and the average decoding accuracies across these iterations were calculated. The decoding accuracy value obtained for a given searchlight was assigned to its central voxel. Individual surface maps containing average decoding accuracies were aligned to the group-averaged mesh using the transformation matrices created during CBA (Section 2.5.2.1.2).

At the group level, we performed a two-tailed one-sample *t*-test across individual maps to identify vertices where classification was significantly above chance (50%, since our classifiers were binary). The resulting map was *z*-scored and corrected using the Threshold-Free Cluster Enhancement with 1000 Monte Carlo simulations (corrected cluster threshold of p = .05; two-

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[14] An individual dataset submitted to decoding analysis consisted of 32 patterns (4 conditions/”targets” × 8 runs).

tailed; $z_{max} = 1.96$) and projected onto the group-averaged surface meshes for visualization purposes.

3. Results

3.1. Behavioral results

Average response latencies for the 12 subjects that participated in the behavioral experiment are reported in Table 3.1.

Condition	**Session 1 (pre-training), RTs in ms (mean ± SD)**	**Session 2 (post-training), RT in ms (mean ± SD)**	**Facilitation effect**
NU (untrained nouns)	850 ± 135	837 ± 157	13 ∓ 22
NT (trained nouns)	819 ± 95	751 ± 140	68 ∓ 45
VU (untrained verbs)	936 ± 125	924 ± 147	12 ∓ 22
VT (trained verbs)	944 ± 114	844 ± 152	100 ∓ 38
Control (scrambles)[15]	681 ± 99	742 ± 156	-61 ∓ 57

Table 3.1: Average reaction times and standard deviations (in ms) in the behavioral experiment. Magnitude of naming facilitation is calculated as the difference between response latencies in the two sessions.

A three-way repeated-measures ANOVA with session (first, second), word class (noun, verb) and training (trained, untrained) as within-subject factors revealed that all three main effects on RTs were significant at $p < .05$. We found that nouns were produced significantly faster than verbs, as evidenced by a **main effect of word class** ($F(1, 11) = 68.89$, $p < .001$). A significant **main effect of training** ($F(1, 11) = 41.22$, $p < .001$) confirmed that trained items were on average produced

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[15] Since we only included scrambled images into the stimulus set to keep the design of the behavioral study as close to the fMRI one as possible and were not particularly interested in reaction times, we did not include them into subsequent statistical analyses. We will just note here that the observed negative "facilitation" effect can be explained by the delayed identification of response onsets in the second experimental session, due to the fact that the target pseudoword /sin:'toti/ used in this session started with a sibilant consonant, whereas that used in the first session started with a plosive consonant (/ber:'tova/).

faster than untrained ones. We also found a significant **main effect of session** ($F(1, 11) = 6.32$, $p = .029$). Response latencies were faster in the second as compared to the first session for all four stimulus subsets (see Fig. 3.4). In addition, the ANOVA revealed a significant interaction between session and training ($F(1, 11) = 10.57$, $p = .008$), which is expected, considering that in the first session (i.e., prior to training) untrained and to-be-trained items were supposed to be indistinguishable.

Graphically the results are presented in Fig. 3.4.

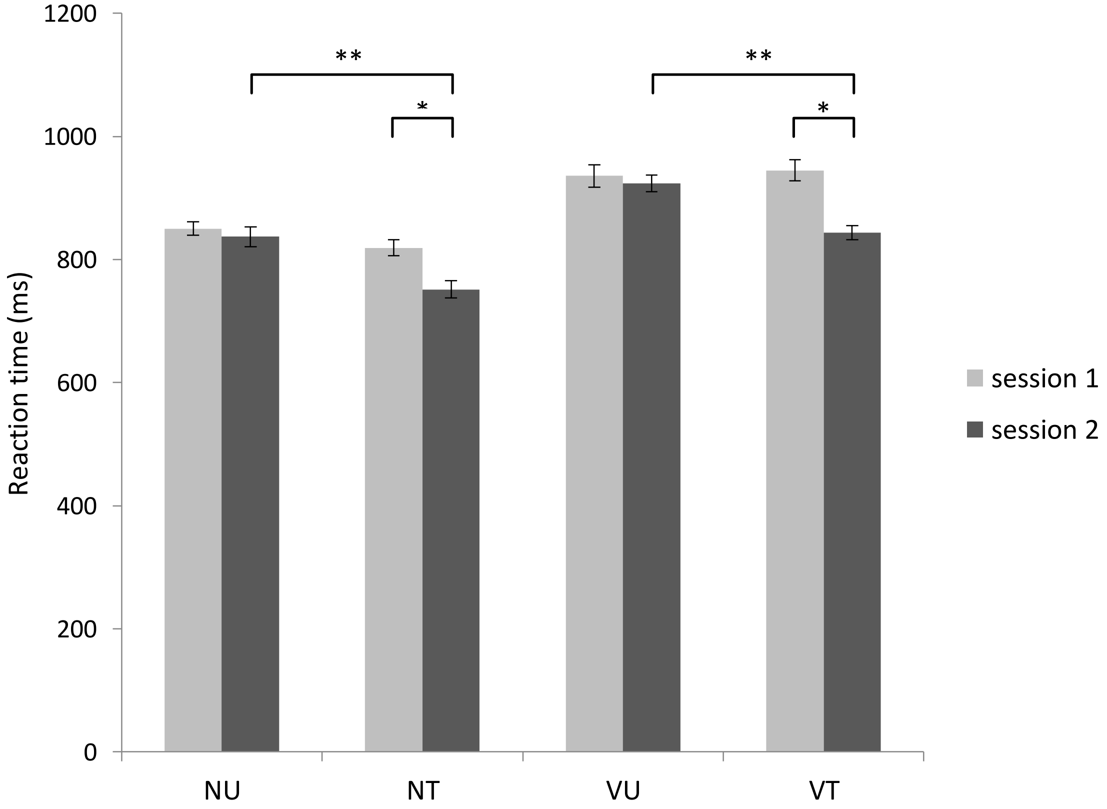

Figure 3.4: Behavioral study results. Average reaction times for each stimulus category in session 1 (light grey bars) and session 2 (dark grey bars). NU = untrained nouns, NT = trained nouns, VU = untrained verbs, VT = trained verbs. Error bars reflect standard errors of the mean after removing between-subject variability (Cousineau, 2005); * denotes significant effects at $p_{FDR} < .05$; ** denotes significant effects at $p_{FDR} < .005$.

In order to examine whether the decrease in RTs in the second session was driven mainly by session or by training effects, we conducted six paired-samples *t*-tests comparing trained and untrained items belonging to the same word class within and across sessions. In addition, for each word class we conducted a *t*-test comparing items from the trained and the untrained subset in session 1, in order to assure that there was no significant difference between the two subsets prior to training. The resulting *p*-values were corrected using the false discovery rate (FDR) method for the overall number of comparisons (n = 8; Benjamini & Yekutieli, 2001). We confirmed the presence of significant training effects in both nouns and verbs in two different ways – by comparing responses to trained items across the sessions, before and after training (S2_NT vs. S1_NT: $p_{FDR} = .026$; S2_VT vs. S1_VT: $p_{FDR} = .01$), and by comparing trained and untrained items in the second, post-training session (S2_NT vs. S2_NU: $p_{FDR} = .003$, S2_VT vs. S2_VU: $p_{FDR} = .004$). However, we did not find significant session effects for either nouns (S2_NU vs. S1_NU: $p_{FDR} = .694$, ns) or verbs (S2_VU vs. S1_VU: $p_{FDR} = .645$, ns), suggesting that the significant main effect of session may have been actually been driven by the training effect. The *t*-tests designed to compare two subsets belonging to the same word class prior to training revealed no significant difference between trained and untrained nouns (S1_NT vs. S1_NU: $p = .154$, ns) or verbs (S1_VT vs. S1_VU: $p = .611$, ns), indicating that stimulus subsets were properly balanced.

3.2. fMRI results

3.2.1. Univariate analyses

3.2.1.1. ROI analysis

We conducted a two-way repeated-measures ANOVA on the data from the second fMRI session, with training (trained, untrained) and word class (nouns, verbs) as within-subject factors, in each of the 10 ROIs selected for analysis. The obtained *p*-values were corrected for the overall number of tests (n = 30) using the FDR method (Benjamini & Yekutieli, 2001). *F*-statistics and *p*-values for all ANOVAs are reported in Appendix B. A **main effect of training** was significant at $\alpha = .05$ in five ROIs – interestingly, however, in different ROIs this effect was opposite in its direction. The BOLD signal was significantly reduced post training in ACC (p_{FDR} = .047), pars triangularis (p_{FDR} = .03) and showed a strong trend toward significance in pars opercularis (p_{FDR} = .053). At the same time, after training the BOLD amplitude increased in PCC (p_{FDR} = .02) and precuneus (p_{FDR} = .023). Additionally, midMTG showed a significant training-related increase (uncorrected p = .039), which, however, did not survive the FDR correction (p_{FDR} = .13, ns). We also found a significant **main effect of word class** in three ROIs (with the BOLD signal being significantly weaker for nouns than for verbs in all three ROIs), including pars opercularis (p_{FDR} = .03), midMTG (p_{FDR} = .035) and postITG (p_{FDR} = .042). No interaction was found between the two effects in any of the regions, suggesting that practice-induced changes were not modulated by word class. Three ROIs (pars orbitalis, postSTG and extrastriate) did not respond to condition manipulation.

Average beta estimates for the four experimental conditions in the seven ROIs that revealed significant main effects of word class and/or training are displayed in Fig. 3.5.

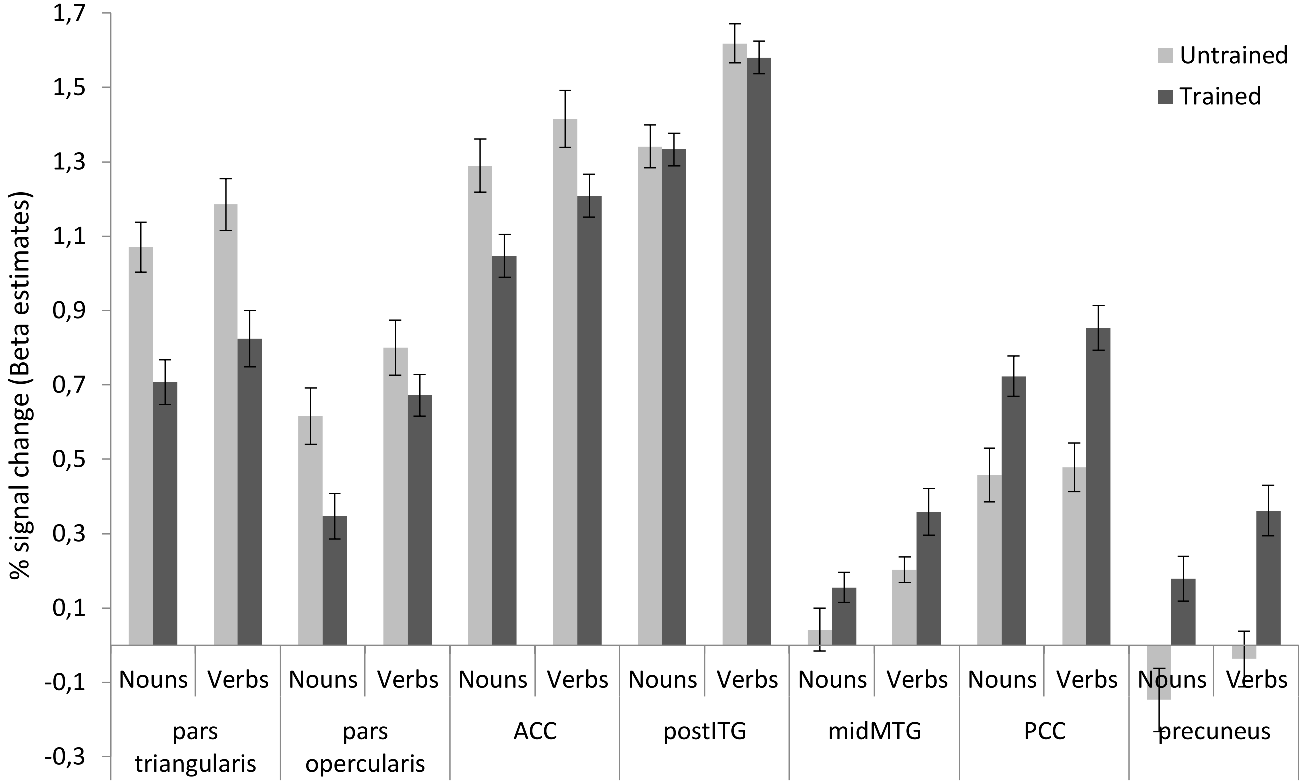

Figure 3.5: Average beta weights for trained and untrained nouns and verbs in seven ROIs that showed a significant main effect of word class (pars opercularis, postITG, midMTG) or a significant main effect of training (pars triangularis, pars opercularis, ACC, PCC, precuneus) in fMRI2. Error bars denote standard errors of the mean after removing between-subject variability (Cousineau, 2005). ACC = anterior cingulate cortex, postITG = posterior inferior temporal gyrus, midMTG = mid-portion of middle temporal gyrus, PCC = posterior cingulate cortex.

3.2.1.2. Univariate whole-brain analysis

3.2.1.2.1. Object and action naming networks. Word class effects

Viewing and naming pictures of real objects and actions activated similar brain networks (Fig. 3.6), as evidenced by contrasting nouns/verbs with phase-scrambled controls in the first fMRI session (S1_NU + S1_NT > S1_Control; S1_VU + S1_VT > S1_Control). Namely, they engaged lateral and ventral occipitotemporal areas, including the inferior and middle occipital gyrus, the fusiform and the parahippocampal gyrus bilaterally, which are together known as the ventral visual processing stream involved in object and shape recognition (the so-called "what" pathway mediating vision for perception; Goodale & Milner, 1992; Ungerleider & Haxby, 1994). These activations extended bilaterally into the posterior portion of the superior parietal lobule, and into the anterior insular cortices. Additionally, picture naming recruited most of the left inferior frontal cortex, including Broca's area, which was expected in the context of a language task, as well as two clusters on the medial surface of the left hemisphere — namely, the anterior supplementary motor area (SMA)[16] and ventral precuneus.

The opposite contrasts (S1_Control > S1_NU + S1_NT, S1_Control > S1_VU + S1_VT; not pictured) revealed significant activation increases in response to meaningless controls as compared to nameable objects and actions in early visual areas, reflecting additional processing load placed on the visual system by phase-scrambled images, as well as in a number of motor (precentral gyrus, central sulcus), auditory (postSTG) and executive (middle and superior frontal gyrus, ACC) regions bilaterally, supporting previous accounts of their role in pseudoword repetition (Vigneau et al., 2006).

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[16] The active clusters in the SMA are located rostrally to the vertical commissure anterior (VCA) line, which divides pre-SMA from SMA-proper, based on anatomical and functional evidence (Picard & Strick, 1996, 2001; Geyer et al., 2000).

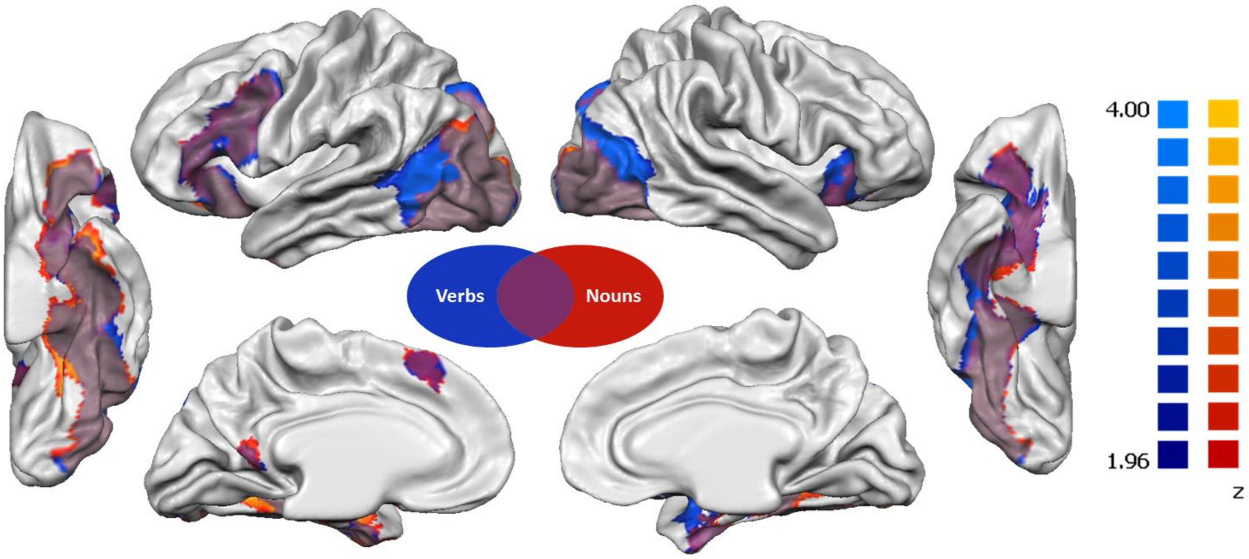

Figure 3.6: Object (orange/red) and action (blue) naming networks, identified by the univariate RFX-GLM contrast of all nouns/verbs with scrambled meaningless images in fMRI1. The logical conjunction of the two maps (i.e., areas activated by both object and action naming) is shown in purple. The statistical group map (n = 20) for each hemisphere was corrected for multiple comparisons using TFCE (α = .05, two-tailed; negative tail not pictured) and projected onto the group-averaged surface meshes for visualization.

The visual comparison of the object and action naming networks suggested that bilateral activations associated with verb production extended more into the posterior middle temporal cortex and the superior parietal lobule (blue clusters on Fig. 3.6). However, the "inter-ocular trauma test" is not a sufficient means of inferential reasoning (see "imager's fallacy" in Henson, 2005). In order to formally confirm our observation, we conducted a direct test of responses to nouns and verbs in fMRI session 1 (S1_VU + S1_VT > S1_NU + S1_NT; Fig. 3.7). It revealed that verb naming engaged to a greater extent the lateral occipitotemporal cortex, including the middle occipital, inferior occipital, middle temporal and superior temporal gyri bilaterally. In addition, the bilateral fusiform/inferior temporal gyrus and left-lateralized regions in the superior parietal lobule and the intraparietal sulcus were more engaged in action, as opposed to object naming. The opposite contrast (S1_NU + S1_NT > S1_VU + S1_VT) showed that only one small cluster — in the posterior portion of the medial fusiform — responded stronger to nouns than to verbs.

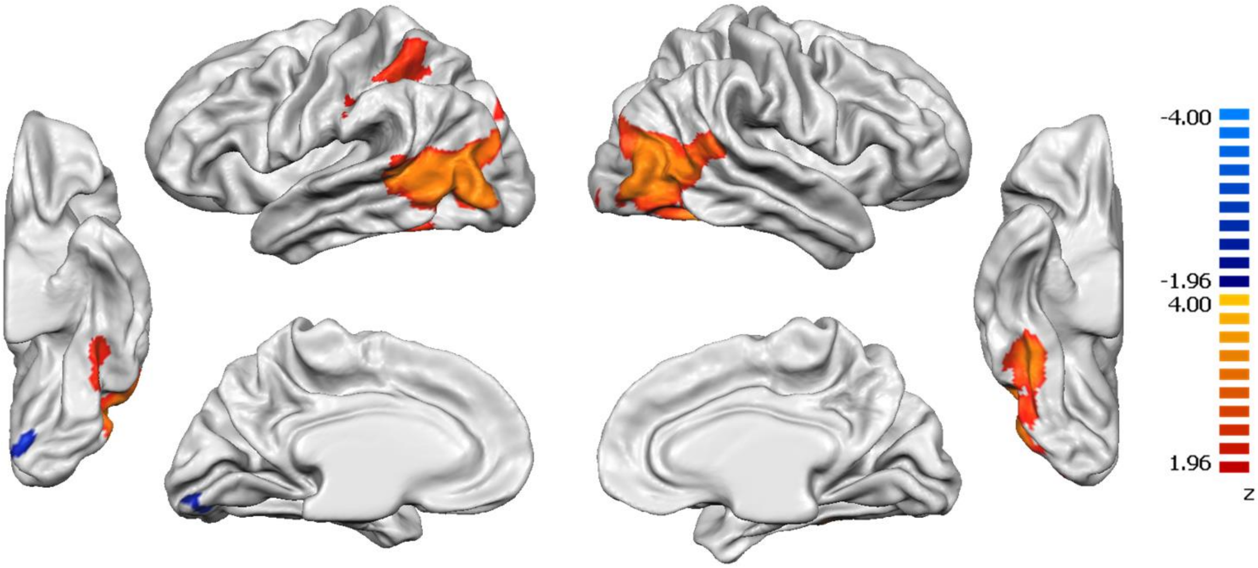

Figure 3.7: Areas showing increased BOLD response to verbs as compared to nouns (orange/red) and to nouns as compared to verbs (blue) in fMRI1, as revealed by the group univariate RFX GLM contrast, corrected using TFCE at α = .05 (two-tailed).

3.2.1.2.2. Training effects

In order to identify the neural correlates of intensive naming practice, we compared responses to trained and untrained items. No significant activations were found when contrasting these items in the first fMRI session (S1_NT > S1_NU; S1_VT > S1_VU), indicating that no differences between the two subsets of words belonging to a given word class existed before the subjects underwent ten-day training of naming. Contrasts of the same items in the post-training session (S2_NT > S2_NU; S2_VT > S2_VU) revealed significant changes in the BOLD amplitude as a function of practice in several brain regions (Fig. 3.8; Table 3.2). Namely, both for trained nouns (Fig. 3.8A) and for trained verbs (Fig. 3.8B), as compared to untrained items in the same post-training session, the BOLD response was significantly reduced in anterior regions of the left hemisphere, including a posterior part of the IFG (pars opercularis/pars triangularis) and the adjacent anterior insula.

The deactivations observed for verbs looked more extensive than those for nouns (cf. Fig. 3.8B and Fig. 3.8A). However, this seeming difference in the magnitude of training effects for the two word classes was not statistically significant, as revealed by the compound contrast (S2_VT > S2 > VU) > (S2_NT > S2_NU).

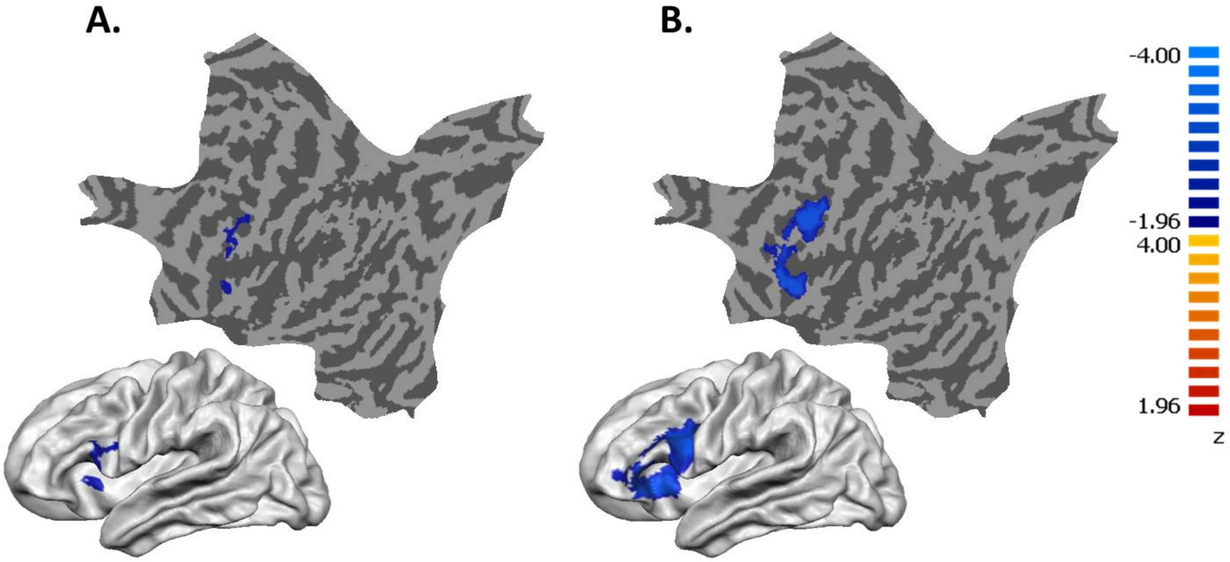

Figure 3.8: Areas of the left hemisphere showing significant deactivation following training of nouns (A) and verbs (B), as evidenced by contrasting items from the trained and the untrained subset in the second fMRI session. The results of the group univariate RFX GLM contrast were corrected using TFCE at α = .05 (two-tailed) and projected on the group-averaged smoothed mesh and the flattened cortical surface of the left hemisphere.

Contrast description and anatomical label	Cluster size (mm^2)	Talairach coordinates			*z*-score	*p*-value
		x	*y*	*z*		
Trained (NT) > Untrained (NU) nouns in fMRI session 2						
left inferior frontal gyrus	116	−43.5	2.4	21.0	−2.05	< .040
left anterior insula	34	−31.0	11.1	3.2	−2.1	< .036
Trained (VT) > Untrained (VU) verbs in fMRI session 2						
left inferior frontal gyrus	540	−40.5	3.7	22.7	−2.88	< .004
left anterior insula	489	−30.5	12.3	2.2	−2.88	< .004

Table 3.2: Talairach coordinates of activation peaks of clusters showing significant activation decreases following training, as evidenced by comparisons of trained and untrained items in fMRI2 (see also Fig. 3.8).

We also examined the training effects by comparing the BOLD response to the same trained items in the two sessions, i.e., before and after they were trained. To rule out the potential contamination of training effects by task habituation, we computed compound contrasts in which we “subtracted” potential session effects (across-session activation changes in response to untrained items) from training effects (across-session activation changes in response to trained items). Across-session effects of verb training ((S2_VT > S1_VT) > (S2_VU > S1_VU)) closely resembled those revealed by the within-session contrast (S2_VT > S2_VU) — namely, significant deactivations were observed in the left posterior IFG (pars opercularis/pars triangularis) and the anterior portion of the insula. The analogous across-session contrast for nouns ((S2_NT > S1_NT) > (S2_NU > S1_NU)) did not yield any significant clusters. Since we already had a hypothesis regarding the direction of activation changes in the left anterior areas, we relaxed the statistical threshold from two-tailed ($z_{\min} = -1.96$) to one-tailed ($z_{\min} = -1.65$). At a looser threshold, the across-session contrast for nouns revealed deactivation in pars triangularis, while the across-session contrast for verbs additionally showed practice-related BOLD decrease in the most anterior portion of the left IFG, pars orbitalis.

3.2.1.2.3. Session effects

Finally, we examined across-session contrasts of items that were not involved in training (S2_NU > S1_NU; S2_VU > S1_VU) in order to see whether the mere exposure to the same stimuli and the same task (in the same scanner environment) twice over the course of roughly two weeks would result in significant priming or task habituation effects. Indeed, in the second session we found significant deactivations in a number of areas, including the primary and secondary visual cortices and the medial fusiform bilaterally, both for nouns (Fig. 3.9A) and for verbs (Fig. 3.9B), as well as the superior parietal lobule (bilateral for nouns and left-lateralized for verbs). Additionally, we detected clusters of decreased activation in the right parieto-occipital sulcus for verbs and in the left posterior superior frontal gyrus (on the lateral surface, adjacent to the precentral gyrus) for nouns. The compound contrast revealed no significant differences in session effects for the two word classes ((S2_VU > S1_VU) > (S2_NU > S1_NU)).

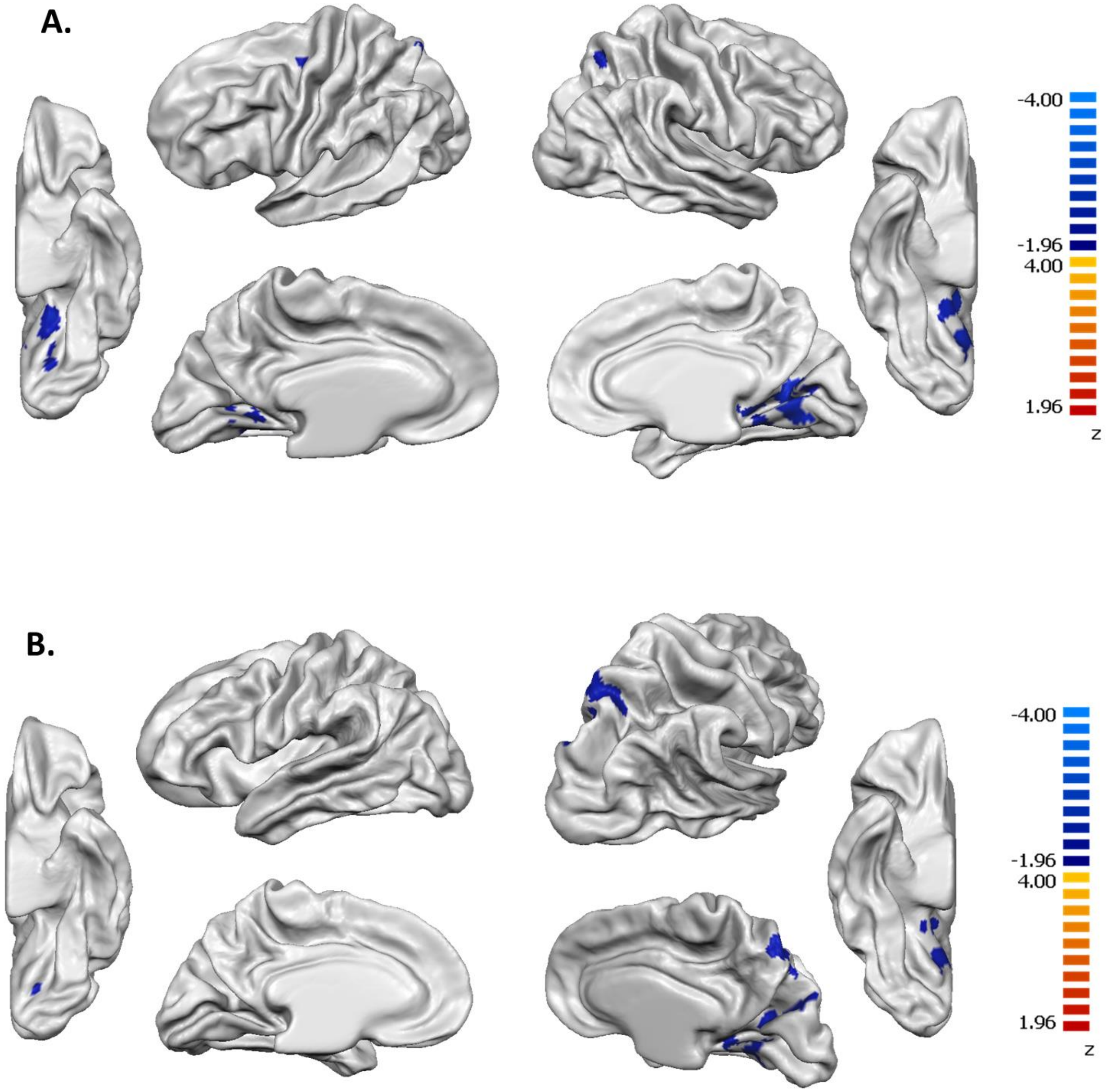

Figure 3.9: Session effects, stemming from task accommodation and stimulus priming, as revealed by the contrasts of untrained nouns (A) and untrained verbs (B) across the two fMRI sessions. The results of the group univariate RFX GLM contrast were corrected using TFCE at α = .05 (two-tailed).

3.2.2. Multivariate analysis

3.2.2.1. Word class effects

We trained the classifier on the data from the first, pre-training, fMRI session to test in which areas it would be able to reliably distinguish between nouns and verbs. The whole-brain searchlight analysis (Fig. 3.10) revealed that patterns of *t*-scores for words of the two classes were decodable in a number of areas, including lateral occipitotemporal and superior parietal regions bilaterally, confirming the results of the univariate analysis (cf. Fig. 3.7). Additionally, nouns and verbs showed different activation profiles in ventral occipitotemporal cortices, early visual areas and precuneus of both hemispheres. Finally, the word class could be predicted by the classifier significantly above chance in the anterior brain regions, predominantly in the left inferior frontal cortex, extending into the middle frontal gyrus dorsally and into the premotor cortex caudally.

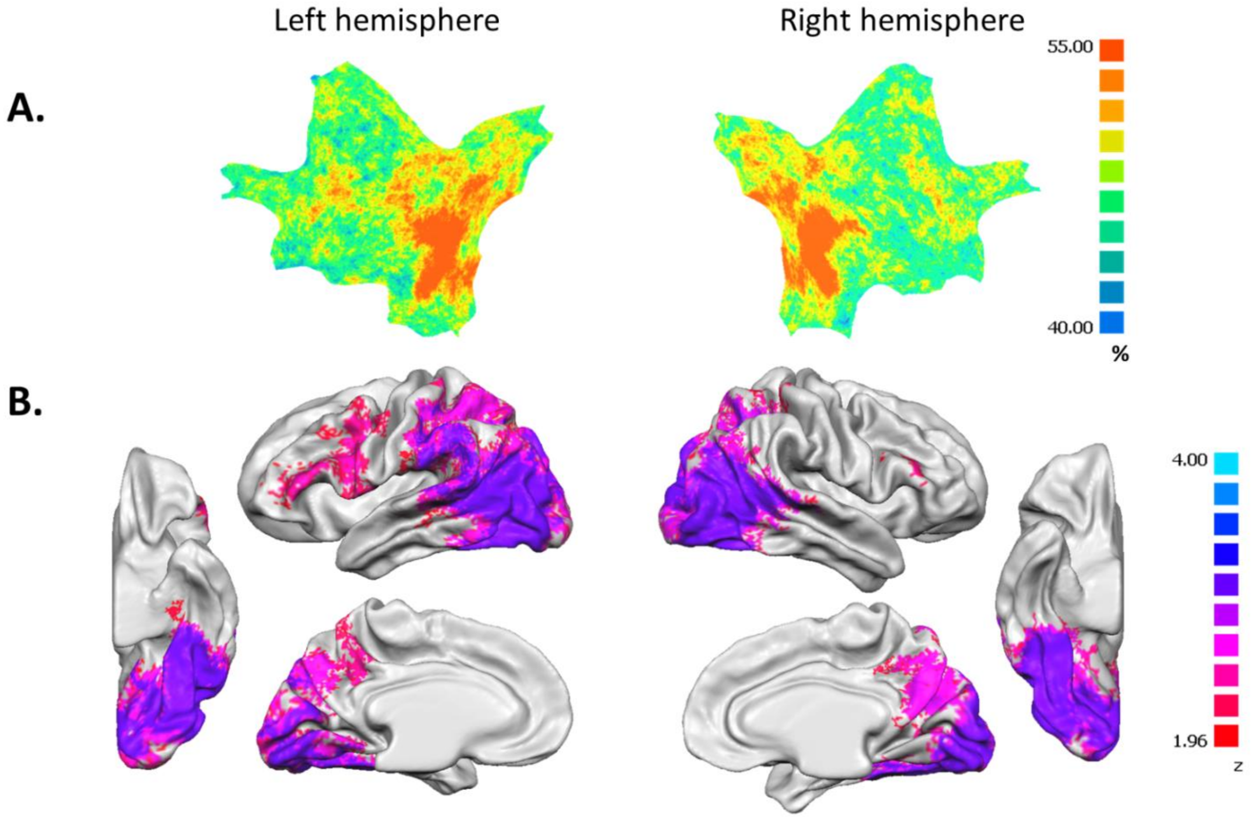

Figure 3.10: Multivariate results. Decoding of word classes, based on the data from fMRI1. A. Mean accuracy maps of the searchlight MVPA. Individual accuracy maps (n = 20) were averaged and projected onto a flattened group-averaged surface. Decoding accuracy at chance is 50%. B. Statistical group maps are corrected using TFCE at $\alpha = .05$ (two-tailed).

Although the decoding analysis proved to be overall more sensitive that the univariate one, it has one significant shortcoming — namely, it can show in which areas the activation profiles are different for the two word classes, but does not tell us for which condition the net BOLD activation is greater in a given region. In order to answer this question, we looked at the uncorrected maps for the univariate contrast of verbs and nouns, described in Section 3.2.1.2.1, thresholded at a liberal $p < .3$. In all of the described areas the overall BOLD activation was greater for verbs than for nouns, with the exception of the early visual areas on the medial surface and the fusiform, which showed noun-related increases.

3.2.2.1. Training effects

We conducted decoding analyses of the training effects using the data from the second, post-training, fMRI session. First, we trained the two classifiers to distinguish between trained and untrained items separately for each word class, but the average decoding accuracies did not go beyond chance in any of the brain regions. This could be explained by insufficient statistical power. In order to increase the power, we collapsed the data across word classes and trained a binary classifier to distinguish between trained and untrained items (irrespective of word class). The results are presented in Fig. 3.11. The regions that were found to be sensitive to training included several temporal and parietal areas in the left hemisphere (posterior MTG, angular gyrus, precuneus). Additionally, decoding was significantly above chance in a cluster in the left anterior insula and in two small clusters in the vicinity of the right calcarine sulcus.

The sensitivity of the left anterior insula to training matches the report of insular decreases in the whole-brain univariate analysis (Section 3.2.1.2.2). The distinguishable activity for the trained and the untrained items observed in the left precuneus must reflect the increased post-training activity in this region, confirmed by the univariate ROI analysis (Section 3.2.1.1).

In order to identify the direction of training-related changes in other clusters, we looked at the uncorrected univariate maps ($p < .3$) for the univariate contrast of trained and untrained items in the second fMRI session. It showed that activity in the left angular gyrus and the left posterior middle temporal cortex, as well as activation in the early visual cortex (V1/V2) of the right hemisphere, was greater for trained as compared to untrained items.

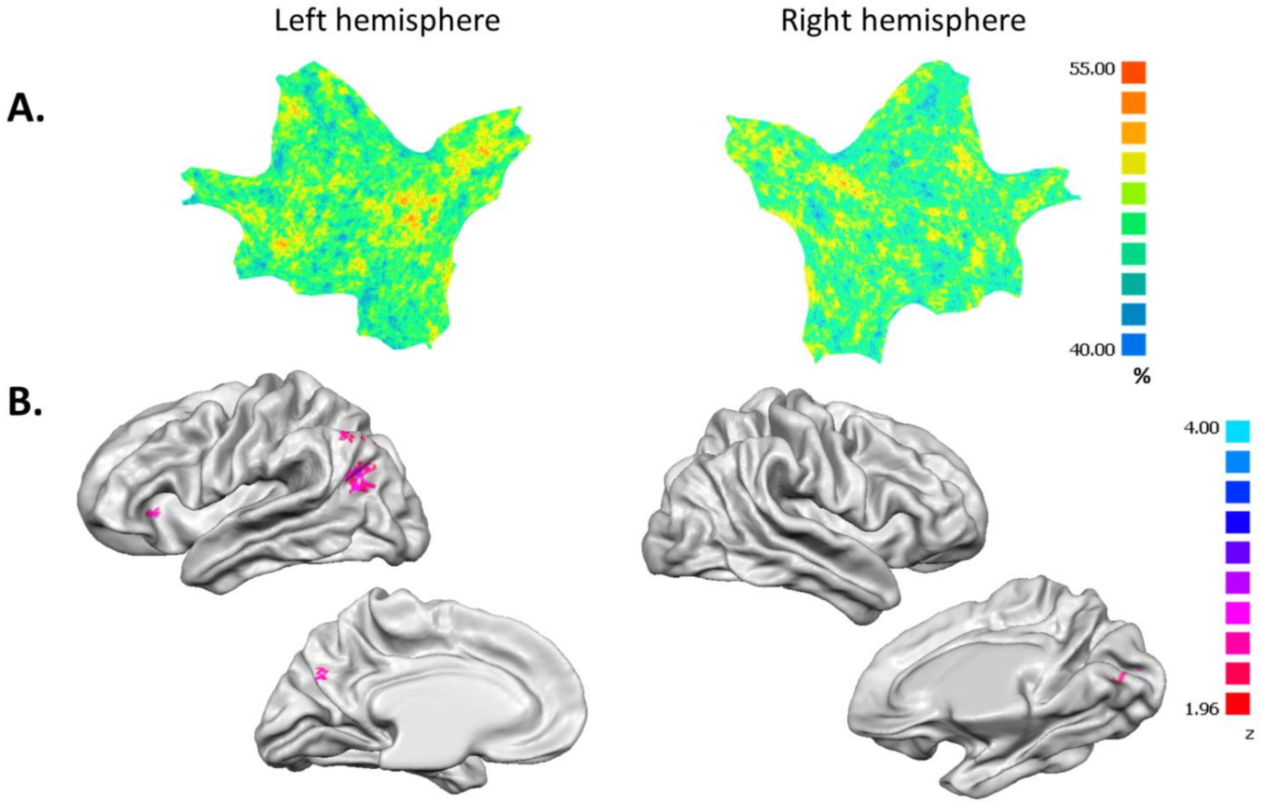

Figure 3.11: Multivariate results. Decoding of trained and untrained items, based on the data from fMRI2. A. Mean accuracy maps of the searchlight MVPA. Individual accuracy maps (n = 20) were averaged and projected onto a flattened group-averaged surface. Decoding accuracy at chance is 50%. B. Statistical group maps are corrected using TFCE at α = .05 (two-tailed).

4. Discussion

4.1. Picture naming network

The univariate contrasts of experimental items with phase-scrambled images in the first fMRI session revealed that naming of objects and actions from pictures engaged similar cortical networks, encompassing lateral and ventral occipitotemporal cortices bilaterally and extending into the inferior frontal gyrus (IFG) of the left hemisphere. Object and action naming activated most of the left IFG (pars orbitalis, pars triangularis, pars opercularis), along with adjacent portions of the middle frontal gyrus, precentral gyrus and the frontal operculum/anterior insula. Additionally, we found activation in two small clusters on the medial wall of the left hemisphere, namely, in the supplementary motor cortex (SMA) and in the inferior part of the precuneus.

Picture naming is a complex process, involving all stages of word production, as well as the lead-in visual recognition processes (Indefrey & Levelt, 2004). By using meaningless scrambled images, in response to which subjects had to produce a pseudoword, as a baseline condition, we aimed to control simultaneously for low-level visual input and for motor output; thus, the observed activations were expected to reflect mainly linguistic processes. Considering the low temporal resolution power of fMRI, obtained activation maps should capture all the other relevant operations involved in spoken word production, including conceptualization, lexical selection, retrieval of the phonological form, syllabification and preparation of articulatory gestures (Levelt, 1999). Although disentangling the activations associated with different cognitive processes is not possible within the context of a picture naming task, insights gained from previous neuroimaging research can help interpret current results. For example, the temporal characteristics of information flow within the naming network were demonstrated using magnetoencephalography (MEG). Liljeström and colleagues (2009) showed that naming of objects and actions from pictures engaged a bilateral network, in which activation originated in the early visual areas and gradually spread anteriorly, via occipitotemporal and parietal, to temporal and, finally, to frontal cortices[17]. Similar activation patterns revealed by our study likely reflect the initial perceptual and conceptual processing of objects and actions in the ventral visual processing stream (the “what” pathway mediating vision for perception; Goodale & Milner,

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[17] Interestingly, in the case of Liljeström et al. (2009) naming-related frontal activations were bilateral.

1992) and the subsequent transfer of information to the perisylvian areas of the language-dominant hemisphere.

Below we discuss in more detail the potential roles played by different “nodes” of the identified picture naming network.

Occipitotemporal cortices

While activity in bilateral extrastriate cortices is associated with visual recognition (Haxby et al., 1994) and visual-attentional processing (Kastner et al., 1998), the more anterior occipitotemporal regions are believed to store abstract, potentially amodal, conceptual representations. More specifically, the ventral temporal cortices, comprising inferior temporal, fusiform and parahippocampal gyri, are implicated in hosting representations of object concepts (for review, see Martin, 2007), whereas the lateral temporal regions, including the posterior portions of middle temporal and superior temporal gyri, mediate conceptual action knowledge (for review, see Lingnau & Downing, 2015). The role of temporal cortex in conceptual processing is discussed in detail in Section 4.2.

Left inferior frontal gyrus

The activation of the left inferior frontal cortex in the naming task was expected, since this area is commonly involved in linguistic processing. The posterior portion of the left IFG, encompassing pars triangularis and pars opercularis, has been deemed crucial for speech production since Paul Broca proclaimed it as “the seat of the faculty of articulated language” (Broca, 1861), as damage to this area was strongly associated with speech deficits. With the advancement of neuroimaging, a large body of evidence has accumulated that implicates Broca’s area in phonological (Poldrack et al., 1999; Zatorre et al., 1992, 1996), semantic (Demb et al., 1995; Poldrack et al., 1999; Roskies et al., 2001; Wagner et al., 2001; Hagoort, 2005), morphosyntactic (Siri et al., 2008; Vigliocco et al., 2011) and syntactic (Grodzinsky & Santi, 2008; Ben-Shachar et al., 2003;

Embick et al., 2000; Friederici, 2004; Musso et al., 2003; Fiebach et al., 2005; but see Rogalsky & Hickok, 2011) tasks.

While the accounts of functional parcellation of this area are inconsistent[18], it cannot be ruled out that different linguistic operations are carried out in succession by the same portions of the left IFG. An interesting piece of evidence for this comes from a recent study performed by Sahin and colleagues (2009). Using intracranial electrophysiology (ICE), a technique that provides both high temporal (milliseconds) and high spatial (millimeters) resolution, they found that the production of inflected nouns and verbs evoked similar activity patterns in Broca's area, which could be decomposed into three separate components, reflecting the sequential processing of lexical (at ~200 ms), grammatical (at ~320 ms) and phonological (at ~450 ms) information.

It should also be considered that, according to some authors, the left inferior frontal cortex is implied in a number of domain-general functions, some of which are crucial for language tasks. Thompson-Schill and colleagues argue that activation of this area during word and sentence processing reflects cognitive control mechanisms, such as response selection (Thompson-Schill et al., 1997, 1999; Snyder et al., 2007) and conflict detection and resolution (Novick et al., 2005). There is also evidence that the left posterior IFG is activated in working memory tasks (Buchsbaum & D'Esposito, 2008; Hickok et al., 2003; Smith & Jonides, 1997). Recent findings suggest that regions subserving domain-general and language-specific functions are closely intertwined in Broca's area, further complicating the interpretation of fMRI studies (Fedorenko et al., 2012).

Supplementary motor area

The supplementary motor area (SMA), which can be defined as the medial portion of area 6, is commonly implicated in learning, planning and execution of complex, coordinated movements (Lau et al., 2004; Penfield & Welch, 1951; Orgogozo & Larsen, 1979; Lee et al., 1999; Krainik et al., 2001). It has been recently proposed that this region could also play an important role in

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[18] E.g., cf. different views on the specialization of the left posterior IFG for semantic and phonological processing in Poldrack et al. (1999), Vigneau et al. (2006) and Amunts et al. (2004).

language. Activation in SMA is often reported in studies of word production, especially in overt speech, suggesting that this region may be part of a circuit mediating articulatory planning (Indefrey & Levelt, 2004). The role of SMA in articulation is emphasized by neuroimaging studies directly comparing overt and covert speech (Huang et al., 2002; Palmer et al., 2001) and by reports of patients with stroke- and surgery-induced lesions to this area, who exhibit various disturbances of speech, ranging from mildly reduced fluency to complete mutism (Ziegler et al., 1997; Bleasel et al., 1996; Pai, 1999; Krainik et al., 2003; Laplane et al., 1977).

However, SMA involvement in covert speech (e.g., Paulesu et al., 1993) implies that it might also mediate a different function. Motor control studies suggest that SMA can be parcellated into at least two functionally distinct subregions. SMA-proper, located posterior to the vertical commissure anterior (VCA) line, would be directly involved in various aspects of movement generation and control. Pre-SMA, situated anterior to it, is considered by some to be a component of the prefrontal cortex rather than a purely motor area (Picard & Strick, 2001; Rizzolatti et al., 1996). Alario and colleagues (2006) proposed that an analogous antero-posterior functional gradient within SMA exists for language. According to their hypothesis, while SMA-proper mediates articulatory motor planning and execution, pre-SMA could be involved in the stages of word production that precede articulatory planning. More specifically, Alario et al. suggest an additional functional subdivision within pre-SMA, in which the posterior portion mediates phonological and syllabic encoding, while the anterior part is involved in lexical selection. The latter suggestion is supported by the findings of Crosson and co-authors (2001), who reported the involvement of the premotor cortex, including pre-SMA, in free word generation, and of Binder and colleagues (2009), who proposed that the left dorsomedial PFC (including a cluster with coordinates very similar to those identified in our study) represents an important node of the semantic network, potentially responsible for semantic retrieval/lexical selection. Interestingly, the posterior boundary of the SMA cluster identified in our naming contrast ($y = 12$) coincides with the coordinate suggested by Alario et al. (2006) as the demarcation point between the word selection and the phonological encoding regions. It is possible, however, that pre-SMA mediates response selection across domains and is not specialized for lexical selection (Tremblay & Gracco, 2009).

Whatever its exact function, this area closely interacts with the classic language regions. Pre-SMA works in parallel with the dorsolateral prefrontal cortex during semantically-based word generation (Crosson et al., 2001; Alario et al., 2006). It is also structurally connected to the perisylvian areas. As shown by studies on monkeys (Geyer et al., 2000; Bates & Goldman-Rakic, 1993), pre-SMA has strong anatomical connections to the dorsolateral prefrontal cortex. In humans, a direct white matter pathway (the so-called 'frontal aslant tract'), connecting the SMA with the classic language regions and their homologues within the posterior IFG, was discovered recently (Vergani et al., 2014; Catani et al., 2012, 2013). Its fibers project from the cortical boundary between the pre-SMA and the SMA-proper to the pars opercularis (BA 44) and, to a lesser degree, to the adjacent pars triangularis (BA 45) and the precentral gyrus (BA 6). This tract is represented bilaterally, but shows a strong left-hemispheric lateralization, reinforcing the idea that it may support language functioning.

Precuneus

The involvement of the precuneus in a naming task may seem puzzling at first. While this region is considered part of the domain-general default mode network (DMN) supporting brain function at rest (Raichle et al., 2001), it is inconsistently activated during language tasks (e.g., Jessen et al., 1999). A meta-analysis by Binder and colleagues (2009) suggests that it may represent a node in the semantic network, mediating the retrieval of conceptual information from memory. Activation could also result from the recollection of episodic memory (Yonelinas et al., 2005; Trinkler et al., 2009) for items previously seen by participants during the preliminary naming session, on one of the days preceding the first scanning session. We will further discuss the potential role of the precuneus in episodic memory in the context of training effects (Section 4.3).

4.2. Word class effects

Results of the behavioral experiment demonstrated that verbs were produced significantly slower than nouns, corroborating previous findings (Vigliocco et al., 2004; Kurland et al., 2018) and suggesting that some aspect(s) of action naming place a greater load on the cognitive system than object naming. Converging evidence from the whole-brain univariate and multivariate fMRI analyses points to bilateral lateral occipitotemporal cortices and predominantly left-lateralized parietal regions as the potential neural loci of these effects. Two of the three left-hemispheric ROIs that showed significant preference for verbs over nouns — namely, midMTG and postITG — overlapped with the anterior and the inferior borders of the univariate left occipitotemporal cluster, respectively. The third ROI that revealed a significant main effect of word class, namely, pars opercularis, also responded to verbs more strongly than to nouns. The same effect in more anterior portions of the left IFG, pars triangularis and pars orbitalis, did not reach significance. Yet, a more sensitive searchlight analysis revealed that verbs could be distinguished from nouns in virtually all left inferior frontal regions engaged in picture naming (cf. Fig. 3.6 and Fig. 3.10).

Lateral occipitotemporal cortices

According to the embodied, or grounded, cognition theories, conceptual knowledge is anchored in the same modality-specific neural systems that subserve high-level action and perception (for reviews, see Barsalou, 2008, 2010; Kiefer & Pulvermüller, 2012). On this view, it is not surprising that the lateral occipitotemporal cortex (LOTC) was more responsive to verbs than nouns, as this area hosts several well-established regions that are implicated in perceptual action processing.

At the core of LOTC is located the human middle temporal (MT) area, also known as the extrastriate visual area V5, which is sensitive to a variety of motion properties, such as direction, optic flow and speed (Tootell et al., 1995; Wall et al., 2008; Lingnau et al., 2009). While MT is implicated in basic motion, activity in the neighboring posterior superior temporal sulcus (pSTS) has been shown to be driven mainly by biological motion (for review, see Puce & Perrett, 2003). Interestingly, both MT and pSTS are sensitive not only to actual motion, but also to motion implied by static images (e.g., Kourtzi & Kanwisher, 2000; Kable et al., 2002), thus accounting for why these areas may be activated by drawings of actions. Another “hot spot” in LOTC, located slightly inferior and anterior to MT, is the so-called extrastriate body area (EBA). Along with the fusiform body area (FBA) in the ventral temporal cortex, this region stores visual representations of human bodies and body parts (Downing et al., 2001), and was also reported to encode shapes of animal bodies (Konkle & Caramazza, 2013). The selective activation of this area during action naming is thus not surprising, as the overwhelming majority of verb stimuli (39/40) depicted people or animals performing various actions[19], whereas most nouns (32/40) referred to inanimate objects. Along with MT, pSTS and EBA, LOTC hosts multiple areas that are activated during both action observation and action execution, and stores information about the type of movement and its perceptual effects, as well as encodes various aspects of knowledge about tools used to perform actions (for review, see Lingnau & Downing, 2015).

However, recent evidence suggests that representations in LOTC may not be strictly perceptual. In fact, the organization of knowledge in this area may follow the antero-posterior abstractness gradient (Kable et al., 2005; Lingnau & Downing, 2015), with the concrete perceptual representations of actions being mediated by occipital areas neighboring MT and the amodal conceptual representations stored in the adjacent lateral posterior temporal cortices (LPTC). Several observations support this hypothesis. First, stronger LPTC activation is obtained not only when participants view pictures/videos of actions as opposed to objects, but also when they read or hear action words, i.e., verbs, as compared to nouns (Kable et al., 2002, 2005; Papeo et al., 2015), suggesting that the role of this region goes beyond visual motion perception. Second, LPTC is sensitive not only to verbs of motion, but also to verbs describing mental states (Bedny et al., 2008, 2012), indicating that its activation during word processing cannot be explained by visual imagery alone and undermining the embodied account of action understanding. Third, the engagement of LPTC in action processing was found in congenitally blind individuals (Bedny et al., 2012), reinforcing the idea that the type of action-related information encoded in LOTC does not rely on visual experience. Fourth, recent neuroimaging experiments employing MVPA have successfully decoded action representations in LOTC that generalize across object exemplars and motion kinematics (Wurm & Lingnau, 2015; Wurm et al., 2016), suggesting that the

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[19] The only inanimate “agent” in the whole stimulus set was a plane taking off the runway.

representations stored in this area are abstract. Finally, the critical role of LOTC in action processing is demonstrated by studies of awake cortical stimulation in patients during picture naming (Corina et al., 2005) and verb generation (Ojemann et al., 2002), and by repetitive transcranial magnetic stimulation (rTMS) in healthy individuals (Papeo et al., 2014). In particular, the latter study showed that rTMS over the left posterior middle temporal gyrus (pMTG) temporarily impaired semantic processing of verbs, but not of nouns, as shown by performance on a synonym judgement task.

Yet, an alternative account suggests that verb-selective activity in posterior temporal regions, and in particular in the left pMTG, may reflect automatic retrieval of lexical or grammatical information associated with verbs (Crepaldi et al., 2011; Willms et al., 2011; Copland et al., 2003; Snyder et al., 2007), rather than conceptual processing of actions they denote. Most studies, including ours, do not allow to tease apart the conceptual and the lexical-semantic accounts, since stimuli consist of prototypical verbs that encode actions and prototypical nouns that refer to objects.

One clever way to disentangle the retrieval of conceptual knowledge from grammatical/lexical information was proposed by Peelen et al. (2012). The study followed a 2×2 design with factors grammatical class (noun, verb) and semantic category (event, state). Peelen et al. found that a region in the left pMTG showed a strong preference for verbs over nouns, irrespective of whether they described an action/event (*'run'*, *'eat'*) or a state (*'stay'*, *'exist'*). At the same time, a portion of pMTG located posterior to the verb-selective cluster was more responsive to action than to state verbs. The important conclusion of Peelen et al.'s study is that the left pMTG may encode both conceptual and linguistic information, with its anterior portion storing knowledge about word class and the posterior portion mediating conceptual representations. More recently, a similar experiment was conducted by Bedny and colleagues (2014). They compared the magnitude of the BOLD response to action verbs and to nouns that described either an object *('alligator'*) or an event *('hurricane'*). They found that a portion of the left pMTG responded more strongly to event nouns than to object nouns, confirming that this area shows preference for action concepts irrespective of the grammatical class. Yet, a more anterior/superior cluster, located at the temporoparietal junction (TPJ), preferred verbs over both object and event nouns, suggesting that this area may be sensitive to some aspect of grammatical class. Taken together, Peelen et al.'s and Bedny et al.'s results indicate that the neural substrates of conceptual/semantic and lexical/grammatical knowledge in LPTC are at least partially separable.

In summary, extant evidence is consistent with an antero-posterior abstractness gradient of action processing in LOTC. While occipital areas, in all likelihood, subserve perceptual processing/visual imagery, temporal regions store conceptual representations of actions, with increasing levels of abstraction in the posterior-anterior direction. Additionally, a distinct cluster in the left anterior pMTG/pSTS may be specialized for processing verbs as a grammatical class. Our results support the latter finding, as occipitotemporal activations during action naming extended more anteriorly in the left pMTG/pSTG, which was not the case for object naming.

Left posterior parietal cortex

Whole-brain analyses revealed that the posterior parietal cortex (left-lateralized in the univariate analysis; bilateral, but predominantly left in the searchlight analysis) was selectively recruited during action naming. The activations encompassed both the superior and the inferior parietal lobules, along with the intraparietal sulcus that divides them. While historically being considered part of the associative cortex that integrates information from different sensory modalities, this brain area was more recently proclaimed the endpoint of the dorsal visual processing stream (the "where" pathway mediating vision for action; Goodale & Milner, 1992). A large body of evidence implicates posterior parietal cortices in space perception and visually-guided prehension movements, such as reaching and grasping. Similar to LOTC in the ventral visual stream, the parietal cortex in humans contains several "hot spots" involved in action planning and execution. Also similar to LOTC, its activation is evoked not only by real actions, but by action-related perceptual tasks, such as action observation, as well as by processing of tools and other action attributes (for review, see Culham & Valyear, 2006).

Activation of the posterior parietal cortex has also been reported in the context of language tasks. In particular, several studies linked it to verb production (Shapiro et al., 2006; Marangolo et al., 2006; Saccuman et al., 2006; Warburton et al., 1996) and recognition (Tsigka et al., 2014). The linguistic nature of the parietal activations in our experiment is indirectly supported by the fact that they were mainly restricted to the left hemisphere. While there is no consensus regarding the role of parietal regions in language tasks, recent studies suggest that this area may be crucial for thematic role assignment (Meltzer-Asscher et al., 2013; Thothathiri et al., 2012). Thus, it is possible that in our experiment posterior parietal activations reflect the automatic retrieval of argument structure of the produced verbs.

A potential confound should be addressed here. Larger activation for verbs in parietal regions could be at least partially attributed to the nature of visual stimuli rather that to a difference in the intrinsic properties of the two word classes. While we tried to balance our object and action drawings for visual complexity and imageability as closely as possible (see Appendix A)[20], the presence of both objects and actions in some of the action pictures could have contributed to their greater perceptual (and conceptual) complexity (for a similar argument, see Crepaldi et al., 2011).

The importance of balancing pictorial stimuli was addressed by Liljeström and colleagues (2008), who compared naming of objects and actions from the same pictures (e.g., for a drawing depicting a man performing an action with an instrument, the target verb would be the name of the action and the target noun would be the name of the instrument). Additionally, they asked subjects to name objects from modified drawings, in which the visual information cueing the action (e.g., actor) was transformed into random lines surrounding an object; by doing so, the authors aimed to control for low-level visual complexity. While naming in all three experimental conditions activated similar brain networks, noun retrieval from action images was associated with significantly greater activation in the (predominantly left-lateralized) network, including the posterior parietal regions, pMTG and the prefrontal cortex, than naming from object-only images. Increased activation in response to an object in an action context may reflect automatic retrieval of conceptual information about depicted actions; at the same time, parietal activations could be attributed to visual search for task-relevant objects (Nobre et al., 1997; Corbetta & Shulman,

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[20] Note that while we have managed to match the four stimulus subsets on objective visual complexity (measured as the image file size after the conversion to GIF format), which likely corresponds to low-level visual processing demands, we failed to balance our stimuli for the subjective visual complexity (calculated as average scores given to drawings by 50 raters), which potentially reflects the distinction in high-level perceptual features.

1998) or an attentional shift toward them (Beauchamp et al., 2001). In other words, perceptual features of stimuli can be held largely accountable for the nature of observed activations, in areas not restricted to the visual cortex.

Left inferior frontal gyrus

As discussed in Section 4.1 (also see Fig. 3.6), both object and action naming relied on the left inferior frontal cortex, supporting previous findings (e.g., Liljeström et al., 2008, 2009; Sörös et al., 2003). However, the direct contrast of the two word categories revealed that verbs recruited this area to a greater extent than nouns. The univariate ROI analysis showed that the BOLD amplitude in the left pars opercularis was greater for verbs than for nouns, while the two more anterior regions (pars triangularis and pars orbitalis) exhibited no significant word class effect. The multivariate searchlight analysis proved more sensitive and successfully decoded verbs from nouns in the whole extent of the left inferior frontal gyrus (IFG).

The association of verb processing with left IFG activation has a long-standing tradition, rooted in neuropsychological findings. The fronto-temporal dichotomy hypothesis (FTDH), put forward by Damasio & Tranel (1993), had linked selective noun retrieval deficits to lesions in the middle and inferior temporal regions and selective verb impairment to damage in the left posterior inferior frontal and precentral gyri. Substantial evidence from neurological patients was accumulated since, in accord with the proposed double dissociation (Daniele et al., 1994; Bak et al., 2001; Tranel et al., 2001; Shapiro & Caramazza, 2003; for review, see Cappa & Perani, 2003). Further supporting the FTDH, the study of cortical mapping in glioma patients by Havas et al. (2015) found that verb processing was more prone to disruption comparing to noun processing following the electric stimulation of Broca's area.

Yet, several case studies have called Damasio & Tranel's hypothesis into question. For example, verb retrieval was spared in a patient with a vast left prefrontal lesion (De Renzi & Di Pellegrino, 1995), but disproportionately impaired in several patients suffering from isolated damage to temporal (Aggujaro et al., 2006; Tranel et al., 2008) or parietal (Silveri & Di Betta, 1997; Silveri et al., 2003) regions, suggesting that the differences between nouns and verbs cannot be reduced to a single factor, but rather stem from disruption at different levels of word processing, including semantic, phonological and syntactic (Black & Chiat, 2003; Cappa & Perani, 2003).

The findings of neuroimaging studies with healthy individuals are even more varied. In line with our results, greater left IFG activation for verbs as compared to nouns was reported by a number of studies on a variety of tasks, requiring picture naming (Berlingeri et al., 2008), word generation (Warburton et al., 1996), semantic judgement (Tyler et al., 2003, 2004; Palti et al., 2007; Bedny et al., 2008), lexical decision (Perani et al., 1999) and morphological processing (Shapiro et al., 2005; Palti et al., 2007). However, other studies failed to find word class differences in the left IFG (e.g., Tyler et al., 2001), whereas some reported the opposite effect, namely, its greater recruitment by noun processing (e.g., Berlingeri et al., 2008; Siri et al., 2008). Noun preference in the left prefrontal cortex was frequently observed in the context of morphological tasks, which led some researchers to propose that the increased left IFG activation might reflect the morphosyntactic demands posed by a given task, rather than grammatical differences *per se*. Berlingeri and colleagues (2008) investigated word class effects in Italian. While the posterior left IFG was predominantly activated by verbs in a picture naming task, it responded more strongly to nouns than to verbs in a grammatical-class switching task, in which participants were asked to derive a noun from a given verb, or vice versa. The authors attributed this discrepancy to different demands in the two tasks. While producing a verb requires attaching one of three possible infinitive markers (*-are*, *-ere*, *-ire*) to a word stem, depending on the conjugation, the choice of a noun suffix/inflection is highly idiosyncratic (*-o*, *-a*, *-ata*, *-azione*, *-amento*) and, thus, places more load on lexical processing. Sensitivity of the left IFG to morphosyntactic demands was confirmed by Siri et al. (2008) who found that naming of action nouns (*mangiata* '(the) eating') recruited it to a greater degree than naming of infinitive verbs (*mangiare* 'to eat') from the same pictures. At the same time, inflected verbs (*mangia* '(he/she) eats') evoked greater response in the left IFG than verbs in the infinitive. Based on the observation that the left IFG was engaged in inflectional and, to an even greater degree, derivational morphology, Siri et al. proposed that activation in this area resulted from morphosyntactic processing (for similar views see also Sahin et al., 2006; Vigliocco et al., 2011). Vigliocco and co-authors (2011) pointed out that morphosyntactic demands vary cross-linguistically, thus affecting activation differences between nouns and verbs in a given language.

Consistent with this possibility, a recent study in Chinese, a language with more complex noun than verb morphosyntax, found increased left prefrontal activation in response to nouns as compared to verbs (Yu et al., 2013).

In our experiment, verbs were produced in the citation form. Therefore, the morphosyntactic complexity account of verb-specific prefrontal activations is unlikely. The observed word class differences in our experiment are more likely related to lexical selection demands, as verbs typically have more synonyms/hyponyms/hyperonims than nouns. Kan & Thompson-Schill (2004) measured fMRI activity in the prefrontal cortex while subjects named pictures of objects with either high (e.g., *apple*, *kite*) or low (e.g., *sofa/couch*, *shirt/blouse*) name agreement. They found that naming of low-agreement pictures was slower and was associated with increased activation in the left IFG as compared to high-agreement pictures, thus supporting the idea that the left prefrontal cortex mediates selection among competing alternatives (Thompson-Schill et al., 1997, 1999). Although picture-name agreement ratings for the four subsets of stimuli in our experiment did not differ significantly[21], this was due to the fact that we accepted synonymous responses as correct, if their usage frequencies in the language were similar. In our sample, alternative labels were observed for only one noun (*sottomarino/sommergibile* ‘submarine’), but for many verbs (e.g., *remare/vogare* ‘row’, *sventolare/sbandierare* ‘wave (a flag)’, *pelare/sbucciare* ‘peel (potatoes)’).

To sum up, while specific task demands, such as morphosyntactic processing (Siri et al., 2008; grammatical-class switching task in Berlingeri et al., 2008) and lexical selection (Kan & Thompson-Schill, 2004; picture naming task in Berlingeri et al., 2008) very likely contribute to the word-class effects observed in the left inferior frontal cortex, as noted in Section 4.1, this area is functionally non-homogenous. Thus, its activation may reflect multiple, simultaneous cognitive processes, both of the domain-general and of the language-specific type (a similar argument see in Crepaldi et al., 2011; Fedorenko et al., 2012). Therefore, intrinsic differences between the two grammatical classes may also have contributed to activation differences in the left IFG in our experiment. Yet, since the picture naming task captures all successive stages of word production,

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[21] Mean picture-name agreement (PNA) ratings for the four stimulus subsets: 96.6 % for trained nouns, 97 % for untrained nouns, 93.8 % for trained verbs, 93.8 % for untrained verbs. The Kruskal-Wallis test deemed the differences between the four subsets non-significant ($\chi^2(3) = 2.158$, $p = .54$). See also Appendix A.

it cannot be reliably established which aspects of lexical processing, if any, contributed to the word class effects in this region. Further investigation into the functional parcellation of the left inferior frontal cortex is called for to address this question.

Ventral occipitotemporal cortices

The searchlight analysis distinguished between nouns and verbs with a greater-than-chance accuracy in the posterior ventral occipitotemporal cortex bilaterally. Inspection of the uncorrected univariate maps for the corresponding contrast suggested that while the inferior temporal gyri showed a preference for verbs, the fusiform gyri responded more strongly to nouns. A cluster in the left posterior fusiform/extrastriate cortex survived the correction for multiple comparisons in the univariate whole-brain analysis (see Fig. 3.7). Noun preference in the fusiform has been previously reported in several studies directly contrasting nouns and verbs (e.g., Shapiro et al., 2005, 2006). It is not surprising, considering that this region is implicated in storing conceptual object representations (for review, see Martin, 2007). A large body of evidence suggests that different perceptual properties and/or conceptual categories of objects are stored in distinct portions of the ventral occipitotemporal cortex, which may explain why the univariate analysis detected only one small noun-preferring cluster in the left posterior fusiform. Since our stimuli were selected from a wide range of semantic categories and included both living objects and various artifacts, their conceptual representations could be scattered along the fusiform.

Medial occipital regions

Finally, the multivariate analysis successfully decoded nouns and verbs on the medial surface bilaterally. An exploratory univariate analysis with a relaxed significance threshold suggested that regions with greater activity for verbs and those showing preference for nouns were intertwined in the early visual cortices (striate and extrastriate). There is no ready account for this observation. In all likelihood, it suggests that while some aspects of visual processing were more complex for action images (as would be expected, considering that action drawings portrayed both actions and objects, as well as elements in the background), for some respects the overall visual complexity was greater for objects. This explanation is plausible, considering that we specifically asked the artist to add more detail to object drawings in order to better match them for visual complexity with actions.

4.3. Session effects

We evaluated the behavioral and BOLD activation effects of repeated exposure to the same task and stimuli (twice over two weeks) by contrasting the items from the untrained subsets in the two experimental sessions. We hypothesized that long-term priming of object and action naming, as well as habituation to the experimental environment, would lead to facilitated performance on the task, which would be reflected in shorter naming latencies and decreased BOLD activation in areas involved in the task. At the behavioral level, the observed facilitation of repeated exposure *per se* was not statistically significant for any of the two word classes — although we found a significant main effect of session in the three-way ANOVA, post-hoc *t*-tests revealed that this effect was mainly driven by the improvement on trained items. On the contrary, the univariate fMRI analysis suggested that a single repetition of nouns and verbs over the course of two weeks was enough to evoke significant BOLD deactivations in a number of areas. Deactivations were similar for nouns and verbs. They were observed bilaterally in the early visual areas and the fusiform, and in the right superior parietal lobule. Repetition effects in the extrastriate and fusiform regions are in close agreement with the previous reports of long-term object priming, and potentially reflect priming of low-level features and of the amodal structural representations, respectively (Schacter & Buckner, 1998; Henson, 2003; for review, see also Chapter 2). Deactivation in the right superior parietal lobule, in turn, could be attributed to the facilitation of visuo-spatial processing of familiar stimuli (Nobre et al., 1997; Corbetta & Shulman, 1998; Beauchamp et al., 2001).

4.4. Training effects

Behavioral results revealed that naming latencies were significantly reduced for trained nouns and verbs, as evidenced both by comparing trained and untrained items in the post-training session and by contrasting the same items from the trained subsets across the sessions.

At the neural level, the 10-day intensive training of naming resulted in a set of similar changes for nouns and verbs, that encompassed regions in the language network as well as areas traditionally considered to be domain-general. Interestingly, while the left anterior regions typically implicated in language processing showed decreased activation following practice, the left parietal and temporal areas were associated with training-related increases.

Training-related deactivations in left anterior regions

Comparisons of trained and untrained items in the whole-brain univariate fMRI analysis revealed that practice-related naming facilitation was accompanied by decreased activation in the left posterior IFG (limited to the pars triangularis and the pars opercularis, i.e., Broca's area) and in the adjacent frontal operculum/anterior insula for words of both classes, replicating the previous findings on nouns (Basso et al., 2013; Meltzer et al., 2009). These results were corroborated by additional analyses in this study. In particular, the univariate ROI analysis confirmed significant post-training deactivations in the left pars opercularis and pars triangularis (along with the decrease in the left anterior cingulate cortex), whereas the whole-brain multivariate analysis successfully distinguished between trained and untrained items in the left anterior insula.

As discussed in Sections 4.1 and 4.2, the activation of Broca's area has been previously ascribed to a number of linguistic functions. While deactivation in this region following practice may in principle reflect facilitation at any stage of word processing, it could also be attributed to the decreased reliance on executive mechanisms, such as response selection and inhibition of competing responses (Thompson-Schill et al., 1997, 1999). Indeed, during training subjects were encouraged to settle on the target word preferred by controls. This may have artificially increased naming agreement of the stimuli which, according to Kan & Thompson-Schill (2004), negatively correlates with left prefrontal activation. On this account, greater practice-related deactivations would be expected for verbs as compared to nouns, since verbs initially had lower naming agreement (see Section 4.2). While there was no statistical difference in the magnitude of training-related changes for the two word classes, their extent was indeed greater for verbs, as shown by the visual comparison of the two maps (cf. Fig. 3.8A and Fig. 3.8B). An alternative account attributes prefrontal deactivations to stimulus-response mapping (Race et al., 2009; MacDonald et al., 2015; for a detailed discussion see Chapter 2).

Left anterior insular activations in the context of language tasks are traditionally interpreted in terms of articulatory preparation (Dronkers, 1996; Baldo et al., 2011). However, the clusters revealed by our univariate and searchlight analyses were located significantly more anterior to "Dronkers's area" (the dorsal portion of the left precentral insular gyrus). Thus, an alternative explanation seems more likely. Basso et al. (2013), who followed a similar ten-day training paradigm, compared the BOLD activations in response to low-frequency nouns, before and after the training, with a control set of high-frequency nouns that were not involved in practice. While prior to training low-frequency items yielded greater activations in the insular and anterior cingulate cortices bilaterally, in the post-training session they were indistinguishable from high-frequency items. Hence, the decreases in the left anterior insula and in the left anterior cingulate cortex (ACC), identified by our univariate whole-brain and ROI analyses respectively, may mimic the frequency effects, as we artificially manipulated the trained items' frequency by subjecting them to intensive repetition. Supporting evidence comes from several previous studies that implicated ACC and insula in naming of low-frequency items (Graves et al., 2007; Carreiras et al., 2006; de Zubicaray et al., 2005; Binder et al., 2005).

Training-related increases in left temporal and parietal regions

Finally, a number of left-lateralized regions in the parietal and temporal cortices showed significantly increased BOLD activation following practice, as revealed by our univariate ROI (precuneus, posterior cingulate cortex) and whole-brain searchlight (precuneus, angular gyrus, pMTG) analyses.

As discussed in the previous sections, the posterior middle temporal cortex is implicated in storage of conceptual and lexical representations. In the context of the training study, the increased BOLD amplitude in this region might reflect strengthened lexical-semantic representations of the practiced items. Interestingly, the intactness of this region was identified as the sole predictor of successful anomia recovery in a lesion-symptom mapping study by Fridriksson (2010; Fig. 4.1, blue sphere), reinforcing its role in word retrieval. Furthermore, as shown by diffusion-weighted imaging (DWI) studies with healthy subjects, posterior lateral temporal regions are tightly connected to Broca's area, both directly, via the arcuate fasciculus, and indirectly, via a pathway that connects the temporal regions with the inferior parietal lobule and the inferior parietal lobule with the prefrontal cortex (see Fig. 3 in Catani et al., 2005; Fig. 2 in Seghier, 2013; for review, see Rogalsky & Hickok, 2011).

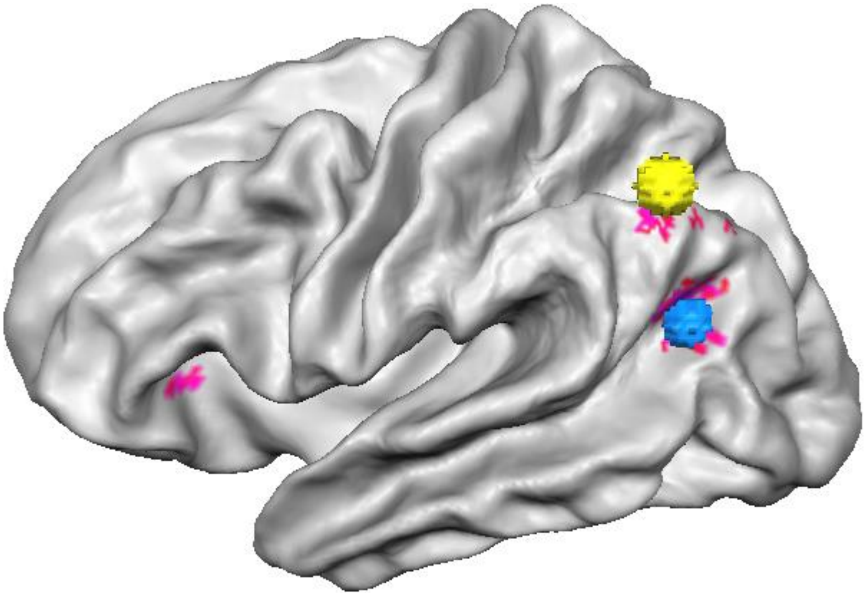

Figure 4.1: Overlapping results of the multivariate analysis of training effects in our study (pink clusters) with the areas identified in a lesion-mapping study of anomia treatment (Fridriksson, 2010; blue sphere, pMTG) and a naming practice study with healthy individuals (Kurland et al., 2018; yellow sphere, angular gyrus). Spheres were created with a 5-mm radius around the peak coordinates reported in the corresponding studies.

Hyperactivation in the precuneus and the posterior cingulate cortex (PCC) has been recently reported by several studies of repeated picture naming in healthy populations (Basso et al., 2013; MacDonald et al., 2015; Kurland et al., 2018) and in patients with aphasia (Heath et al., 2015; Fridriksson, 2010; Fridriksson et al., 2007). Earlier studies of primed naming (see Chapter 2 for review) failed to find training effects in the medial parietal regions, because they restricted their analyses to the classical language regions and/or because of insufficient statistical power/intensity of practice. Inactivation of the precuneus and PCC, along with the angular gyrus, were also reported following sentence repetition (Hasson et al., 2006; Poppenk et al., 2016). Kurland and colleagues (2018) found that a portion of the inferior parietal lobule, closely overlapping with the angular gyrus cluster identified by our study, showed practice effects following several repetitions of nouns and verbs (Fig. 4.1, yellow sphere).

The activation of the medial parietal regions has been attributed by the above mentioned studies to explicit memory for practiced items. The findings of Schott et al. (2005), who reported that conscious recognition of previously studies items was associated with increased activity in the precuneus and PCC, whereas priming in the absence of explicit memory did not reveal such effect, are in agreement with this interpretation. Our results also favor this hypothesis. As evidenced by the analysis of percent signal changes in the ROI analysis, while for untrained items activity in the precuneus was indistinguishable from baseline (it was significantly lesser for nouns; see Fig. 3.5), trained items exhibited a significantly greater BOLD activation than at baseline.

While the precuneus and PCC form the core regions mediating episodic memory retrieval (for review, see Spaniol et al., 2009), the supporting role of the angular gyrus in this process was highlighted recently (Yazar et al., 2012; Seghier, 2013). Importantly, fibers from the angular gyrus project both to the domain-general regions implicated in long-term memory, including precuneus and PCC, and to the inferior frontal cortex (see Fig. 2 in Seghier, 2013), which makes this area perfectly suited to mediate language learning.

It is worth mentioning that the precuneus, PCC and the angular gyrus have been reported to mediate not only episodic, but also semantic memory (Binder et al., 2009; Fairhall & Caramazza, 2013). This is in line with a recent report that the two forms of long-term memory partially rely on the same neural circuit (Burianova et al., 2010).

In conclusion, we should note that the overall training effects could be also considered from the perspective of dynamic changes in large-scale brain networks (Bressler & Menon, 2010). Within this reference frame, activation in the network mediating executive control (prefrontal cortex) and the so-called “salience network”, which is sensitive to stimulus novelty (anterior cingulate, insula), decreases as a function of practice. By contrast, activation in the default mode network (DMN; precuneus, posterior cingulate, angular gyrus), that shows highest metabolism during rest and is associated with processing of internally-generated stimuli (Buckner et al., 2008), increases following training. Increased activity in the DMN in the context of a training study may be interpreted in two ways. On the one hand, practice results in faster responses, which gives participants more time to attend to their own thoughts (even unrelated to the task at hand) during the epoch in which the BOLD signal is measured (Poldrack, 2000). However, the results of Kurland et al. (2018), who observed practice-related inactivations of the precuneus and the angular gyrus despite their use of “variable” epochs, set equal to the naming latencies, speak against this interpretation. Thus, activations in the parietal areas are more likely to reflect the retrieval from episodic memory of memories related to trained items.

Chapter 4. Neural correlates of verb transitivity: An fMRI study

1. Introduction

As we have seen in Chapter 3, words belonging to different semantic/grammatical classes, such as nouns and verbs, rely on partially distinct neural substrates. However, far from representing monolithic entities, these word classes can be subdivided into smaller categories based on their semantic and syntactic properties.

Substantial research in the field of theoretical linguistics in the past few decades has focused on factors that allow sorting of verbs into classes based on their syntactic and semantic properties (Pinker, 2009; Levin & Rappaport Hovav, 2005). Recently, there has been a surge of interest in the neural underpinnings of categorical distinctions in verb representation (e.g., Kemmerer et al., 2008; Kemmerer, 2014). Probably, the main focus in research to this day has concentrated on verb transitivity — i.e., the number of thematic roles a verb can assign. While transitive verbs encode two participants of an action (an actor and an undergoer/goal of an action, e.g., *Johnny reads a book*), intransitive verbs refer to an action/event that has only one participant (either a volitional agent, as in *Johnny runs*, or a passive undergoer, as in *Johnny sleeps*). Thus, it seems reasonable that processing of transitive sentences places a greater load on the cognitive system, as these sentences are more complex syntactically. This view is supported by clinical findings in individuals with aphasia, indicating that sentence production deficits correlate with argument structure complexity. Cross-linguistic data suggest that the number of errors in sentence production tasks increases with the number of thematic roles the predicate assigns. On average, aphasic speakers experience greater difficulties with the production of transitive (two-argument) and, to an even greater extent, ditransitive (three-argument, as in *Johnny puts a book on the shelf*) sentences, as compared to intransitive ones, as evidenced by findings in English (Thompson et al., 1997), Dutch (Bastiaanse & Jonkers, 1998) and Russian (Dragoy & Bastiaanse, 2010). Importantly, some patients experience greater difficulties with transitive and ditransitive verbs even when they are produced in isolation (Kim & Thompson, 2000; Collina et al., 2001), supporting the lexicalist view that information pertaining to the argument structure is stored in the lexicon and is accessed prior to sentence construction (Jackendoff, 1972; Horvath & Siloni, 2011). However, the reports of patients who experience problems with producing a correct argument structure in the absence of verb naming difficulties (e.g., JM, Webster et al., 2004) suggest that not all aspects of the argument structure are necessarily stored in the verb's lexical entry (*lemma*).

The growing number of neuroimaging studies with healthy individuals focus on the neural underpinnings of different characteristics of argument structure (for review, see Thompson & Meltzer-Asscher, 2014) and on the processing conditions under which they are retrieved (Malyutina & den Ouden, 2017). While several aspects of argument structure complexity received attention in the recent literature, including the particular processing demands placed by verbs with multiple thematic options (Shetreet et al., 2007; Shetreet et al., 2010b; Meltzer-Asscher et al., 2015) and by unaccusative verbs (Shetreet et al., 2010a; Meltzer-Asscher et al., 2015), the majority of neurolinguistic studies so far have been devoted to the neural correlates of verb transitivity, or number of verb arguments. These studies show that processing of transitive vs. intransitive verbs in sentential contexts is associated with increased activation in a number of areas, including bilateral superior temporal sulci (Ben-Shachar et al., 2003) and the right anterior cingulate cortex and precuneus (Shetreet et al., 2007). Moreover, mirroring the findings in aphasic patients, recent fMRI evidence from healthy adults indicates that transitivity effects arise already at the single-word level, potentially reflecting differences in lexical-semantic aspects of verb processing. These effects were reported both in verb comprehension (lexical decision tasks in Thompson et al., 2007, 2010; Meltzer-Asscher et al., 2015) and in verb production (picture/video naming task in den Ouden et al., 2009), and encompassed the left (or bilateral) temporoparietal regions, including the posterior middle temporal, angular and supramarginal gyri (both in production and comprehension), as well as Broca's area (only in production). Yet, at present there is no unified account regarding what function is attributed to each area within this widely distributed cortical network.

The understanding of neural mechanisms supporting argument structure retrieval has direct implications for therapy of verb and sentence deficits in aphasia. In particular, as argued by

Webster & Whitworth (2012), determining whether argument structure is lexically specified could help to adopt optimal verb retrieval therapy protocols and potentially resolve the current debates around whether it is more beneficial to treat verbs in isolation or in sentential context, whether one should specifically target argument structure in speech therapy[22], etc.

Only one fMRI study, to our knowledge, examined neural activity associated with successful argument structure processing in individuals with aphasia. Thompson et al. (2010) compared the performance of older healthy listeners and age-matched agrammatic speakers on a lexical decision task. The results of both groups largely replicated those previously reported for healthy young adults (Thompson et al., 2007) — namely, verbs with more complex argument structure recruited the angular gyrus to a greater degree. However, while for the healthy participants this activity was bilateral, in three out of five patients (who performed the task with accuracy comparable to that of healthy controls) it was restricted to the right hemisphere, likely because these patients' lesions extended to the left temporoparietal region.

Tangential evidence regarding the mechanisms supporting argument structure processing comes from a series of studies by Cynthia Thompson and colleagues, dedicated to training of passive sentence processing in agrammatism. According to their hypothesis, the deficit in passive sentence production, commonly observed in agrammatic patients, may arise not (solely) from a morphological deficit, but also due to a structural level impairment pertaining to thematic role assignment (Faroqi-Shah & Thompson, 2003). Eyetracking data seem to favor this hypothesis, as agrammatic patients tend to make longer fixations on the first-mention argument of passive sentences, which are grammatically correct, but in which the roles are erroneously reversed (Cho & Thompson, 2010). As demonstrated by Mack et al. (2017), following successful therapy of passive sentences, the patients' gaze gets to resemble that of unimpaired controls. Preliminary results of an fMRI study with the same agrammatic patients (Thompson et al., in preparation) link the behavioral improvement of their performance on passives with the post-training BOLD

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[22] E.g., if the lexicalist view is correct and argument structure is lexically specified, semantic verb therapy engaging argument structure relations should be most beneficial, both for verb retrieval and sentence production (Mitchum & Berndt, 2001). At the same time, if argument structure is included in a verb's lexical entry, one could expect that explicit cueing of arguments would only lead to improvement on treated items, and would not result in generalized gains. At the present moment, it remains uncertain whether greater improvement of connected speech (and, thus, of the overall quality of a patient's life) could be achieved by treating single verbs, concomitant verb and argument structure therapy or by verb retrieval in sentential contexts (Webster & Whitworth, 2012).

increases in the right superior temporal and supramarginal gyri. Thus, it seems that homologues of the left temporoparietal areas that were implicated in argument structure processing and thematic role assignment by previous studies overtake the function of the damaged hemisphere, when the ability to produce syntactically and semantically correct passive sentences is recovered. However, it should be noted that this functional plasticity was observed only in a subset of participants (4/9), and it is not certain if this pattern would hold if more subjects were added to the analysis. One should make a remark here that finding common denominators in studies with aphasic patients is a challenging task, as the observed behavioral deficits and brain activation patterns can be affected by a variety of factors pertaining to the lesion (site, extent of cortical atrophy, cerebral perfusion and white matter integrity), as well as subject characteristics.

Undoubtedly, in order to interpret the changes associated with treatment of verbs, and argument structure in particular, one needs to rely on the "baseline" data obtained from the healthy controls. Given that the existing reports of the neural underpinnings of verb argument structure in the normal brain are still rather few and are somewhat inconsistent, we conducted our own picture naming experiment with a group of healthy young participants, aiming to test whether we could replicate the previous findings made by den Ouden et al. (2009) on a similar task and to contribute to the body of neuroimaging evidence that could serve as a baseline for comparison for future neuroimaging studies in aphasic patients.

2. Materials and methods

2.1. Participants

Neuroimaging data were gathered from 20 young, neurologically intact volunteers. They were all native speakers of Italian, and were recruited in accordance with the selection criteria outlined in Section 2.1 of Chapter 3. Data from each subject were acquired in two fMRI sessions conducted on separate dates, each consisting of eight functional runs. Due to technical reasons, four runs of two subjects had to be excluded from analyses. Thus, a total of 312 functional runs were entered into the group analyses (20 subjects × 8 runs × 2 sessions, minus 4 runs × 2 subjects).

Behavioral data were collected in a separate study conducted with a group of age-matched participants (n = 12).

2.2. Stimuli and task

Thirty-six drawings, depicting 18 intransitive (containing one argument) and 18 transitive (two-argument) actions, were selected from the image database described in Section 2.2.1 of Chapter 3. The two subsets of pictorial stimuli were balanced for naming agreement and objective visual complexity (measured using the GIF compression method; Forsythe et al., 2008). Additionally, the target verbs were matched on familiarity, imageability and age of acquisition, using subjective ratings obtained from a separate group of native Italian speakers. For the complete list of stimuli refer to Appendix C.

In the behavioral experiment, each trial lasted 5 s. In the fMRI experiment, however, trial duration was randomized using temporal jittering, in order to optimize the efficiency of the experimental design (Watanabe et al., 2013). Pictures were presented for 2 s in the fMRI experiment and for 3 s in the behavioral experiment. A black fixation cross, indicating the onset of a trial, was presented for a period varying between 2 and 5 s in the fMRI experiment and for 2 s in the behavioral experiment. While participants in the behavioral experiment were instructed to respond as soon as they saw a picture, which allowed us to collect reaction times (RTs), the subjects of the fMRI experiment were asked to delay their responses until a green fixation cross appeared on the screen, marking the onset of the response window (3.5 s). This strategy was adopted in order to minimize potential motion artifacts stemming from jaw movement during articulation. The inter-trial interval (ITI) was set to 1 s in the behavioral experiment and was jittered between 0.5 and 1 s in the fMRI experiment. Blank trials were placed at the beginning and at the end of a functional run (5 s in the behavioral experiment, 12 s in the fMRI experiment).

Stimuli were presented in a pseudorandomized order using the ASF toolbox for MATLAB (Schwarzbach, 2011). In order to increase statistical power, all stimuli were presented twice within a session, i.e., four times in total.

2.3. Data acquisition and analysis

2.3.1. Behavioral data

Vocal responses were collected using the Samson Q4 microphone with a low-noise microphone cable (Thomann, UK). RTs were measured automatically using the function supplied with ASF. Recordings were digitized at a sampling rate of 44.1 kHz.

Voice onset intensity threshold was calibrated for each subject individually based on the visual inspection of wave plots of vocal responses that were produced by the ASF software for each trial. RTs deviating from a subject's mean by more than two standard deviations were considered to be outliers and were removed from the analysis (10.1% of the data were removed, including 8.8% of intransitive and 11.3% of transitive trials). After the individual descriptive statistics were calculated in MATLAB R2015b, the data were submitted to a paired-samples *t*-test in SPSS 17.

2.3.2. fMRI data

Structural (MPRAGE) and functional data were collected on a 4 Tesla Bruker MedSpec scanner (Bruker BioSpin MRI GmbH, Ettlingen, Germany) with an eight-channel birdcage head coil, using the acquisition sequences described in Section 2.4.2 of Chapter 3. Subsequently, data were preprocessed in BrainVoyager QX 2.8.4 (Brain Innovation B.V., Maastricht, the Netherlands) in combination with the NeuroElf toolbox for MATLAB (v. 1.1; Weber, neuroelf.net), following a protocol outlined in Section 2.5.2 of Chapter 3 (three volumes at the beginning of a run were discarded; slice timing correction; 3D motion correction; temporal high-pass filtering; spatial smoothing with a FWHM of 6 mm for the univariate analysis, no smoothing for the multivariate analysis). The univariate and multivariate analyses were conducted on the cortical surface, with the aid of cortex-based alignment (CBA), a procedure that allows to improve intersubject alignment of structural and functional data (Fischl et al., 1999; Goebel et al., 2006). To this end, the white/grey matter boundary was reconstructed on an individual Talairach-transformed T1-weighted structural scan of each subject and two 3D meshes were reconstructed, separately for each hemisphere. Next, each mesh was inflated to a sphere with four cortical curvature maps with different levels of smoothing projected onto it and subsequently aligned to a standard spherical surface using a coarse-to-fine moving target approach. Transformation maps obtained as a result of this procedure were used to create two group-averaged surface meshes, for the left and the right hemisphere.

Mesh time courses were created from volume time courses (smoothed for the univariate analysis, unsmoothed for the multivariate analysis) by sampling the functional data from -1 to 2 mm from the reconstructed white/grey matter boundary.

2.3.2.1. Univariate analysis

The data were analyzed with a general linear model (GLM), as implemented in BrainVoyager. A trial was modelled as an epoch lasting from picture onset to picture offset (2 s). Two regressors of-interest corresponded to the two experimental conditions — "transitive verb" and "intransitive verb". Additionally, 6 motion parameters obtained during motion correction were included in the model as regressors of-no-interest. Each predictor was convolved with a dual-gamma hemodynamic response function (HRF; Friston et al., 1998).

Statistical analyses were performed on the cortical surface, separately for each hemisphere. At the first level of statistical analysis, we ran individual fixed-effects (FFX) GLMs in subject space (i.e., prior to CBA) and obtained *t*-statistics for the transitive and the intransitive condition. These *t*-maps were subsequently aligned to the group-averaged meshes using the transformation matrices created during CBA. At the group level, individual CBA-transformed *t*-maps were stacked together and submitted to the permutation analysis. The statistical map for the transitive vs. intransitive contrast was *z*-scored and corrected for multiple comparisons using Threshold-Free Cluster Enhancement (TFCE, Smith and Nichols, 2009), as implemented in the CoSMoMVPA toolbox (Oosterhof et al., 2016). A total of 5000 Monte Carlo simulations and a corrected cluster threshold of $p = .05$ (two-tailed; $z_{\text{min}} = -1.96$, $z_{\text{max}} = 1.96$) were used. The maps obtained for each hemisphere were projected onto the group-averaged hemispheric meshes for visualization.

2.3.2.2. Multivariate analysis

In addition to univariate analysis, we performed a whole-brain searchlight analysis (Kriegeskorte et al., 2006) on the brain surface (Oosterhof et al., 2011), using a linear discriminant analysis (LDA) classifier, as implemented in CoSMoMVPA (Oosterhof et al., 2016). This analysis aimed to test in which brain regions the classifier would be able to decode transitive and intransitive verbs with a greater-than-chance accuracy.

To this end, we ran GLMs separately for each experimental trial. At the single-subject level, *t*-maps with statistics computed trial-wise were stacked together[23] and submitted to the searchlight analysis with an 8 mm radius. Classification accuracies were obtained using a leave-one-out cross-validation method. A classification chunk was defined as six consecutive patterns/trials, with three consecutive trials belonging to each of the two conditions[24]. The decoding accuracy value obtained for a given searchlight was assigned to its central voxel. Individual surface maps containing average decoding accuracies were aligned to the group-averaged mesh using the transformation matrices obtained during CBA.

At the group level, we performed a two-tailed one-sample *t*-test across individual maps to identify vertices where classification accuracy was significantly above chance (chance value was set at 50%, since our classifier was binary). The resulting map was *z*-scored and corrected using the Threshold-Free Cluster Enhancement with 5000 Monte Carlo simulations (corrected cluster threshold of $p = .05$; two-tailed; $z_{\max} = 1.96$) and projected onto the group-averaged surface meshes for visualization purposes.

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[23] I.e., each trial of each run was modelled as a separate predictor, yielding a total of 144 predictors/patterns (36 experimental trials × 2 repetitions per session × 2 sessions).

[24] Thus, for most subjects (18/20) the dataset was split into 24 chunks (144 patterns / 6 patterns per chunk). Datasets of the two remaining subjects, for whom only three stimulus repetitions were included in the analysis (see Section 2.1), consisted of 108 patterns (36 experimental trials × 3 repetitions in total) and 54 chunks (108 / 6).

3. Results

3.1. Behavioral results

As we expected, intransitive verbs (mean ± SD: 889 ± 137 ms) were named faster than transitive (914 ± 117 ms). However, the difference in RTs for the two conditions was not statistically significant ($t(11) = 1.89$, $p = .085$).

3.2. fMRI results

3.2.1. Univariate analysis

The direct contrast of transitive and intransitive items in the univariate analysis revealed, in line with our prediction, that naming of transitive verbs was associated with greater BOLD activations in a number of brain areas (Fig. 4.1). These activations encompassed most of the left intraparietal sulcus (IPS), stretching from the postcentral gyrus ventrally to the superior parietal lobule (SPL) dorsally, as well as two homologous clusters in the right SPL. The middle occipital gyrus (MOG) was activated bilaterally. In the left hemisphere this activation was more pronounced, and extended into the inferior occipital gyrus. Portions of the (predominantly left) ventral occipitotemporal cortex, including the inferior temporal gyrus and the fusiform, also showed a significantly greater response to transitive than intransitive verbs. Finally, a small cluster in the left pars opercularis of the left inferior frontal gyrus (IFG)/ precentral gyrus (BA 44/ BA 6) was more active in the transitive condition.

At the same time, the BOLD amplitude in response to intransitive verbs was higher in several clusters of the right temporoparietal junction (TPJ), including the supramarginal and angular gyri.

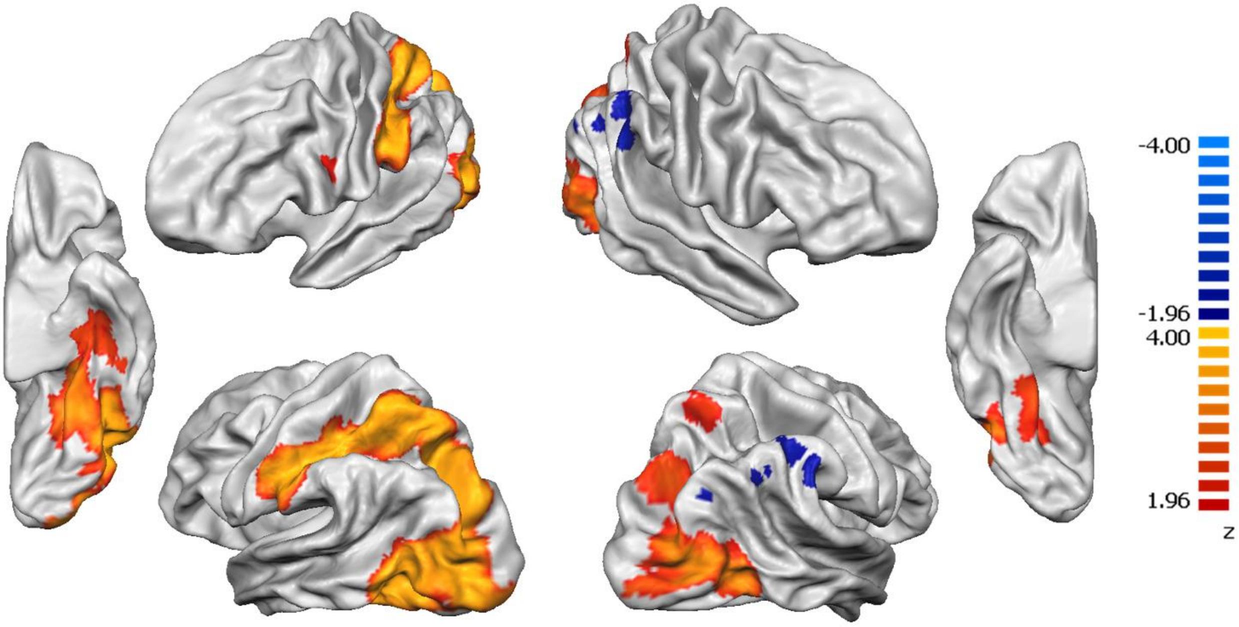

Figure 4.1: Areas showing greater activation in response to transitive (yellow/red) and intransitive (blue) verbs, as identified by the group univariate RXF GLM contrast, corrected using Threshold-Free Cluster Enhancement (TFCE; Smith & Nichols, 2009) at α = .05 (two-tailed).

3.2.2. Multivariate analysis

The results of the searchlight analysis (Fig. 4.2) were virtually identical to those identified by the GLM (cf. Fig. 4.1). The classifier successfully decoded transitive and intransitive items in all regions that showed a significant effect in the univariate analysis, with the exception of the right TPJ. Overall, however, the statistical maps produced by the MVP analysis were more extensive, especially in the left hemisphere. Namely, the left-hemispheric prefrontal cluster, that showed greater activation in the transitive condition, was larger and extended more anteriorly. At the same time, the left temporal activations extended more into the posterior middle temporal gyrus (MTG) and the neighboring superior (STG) and inferior temporal (ITG) gyri.

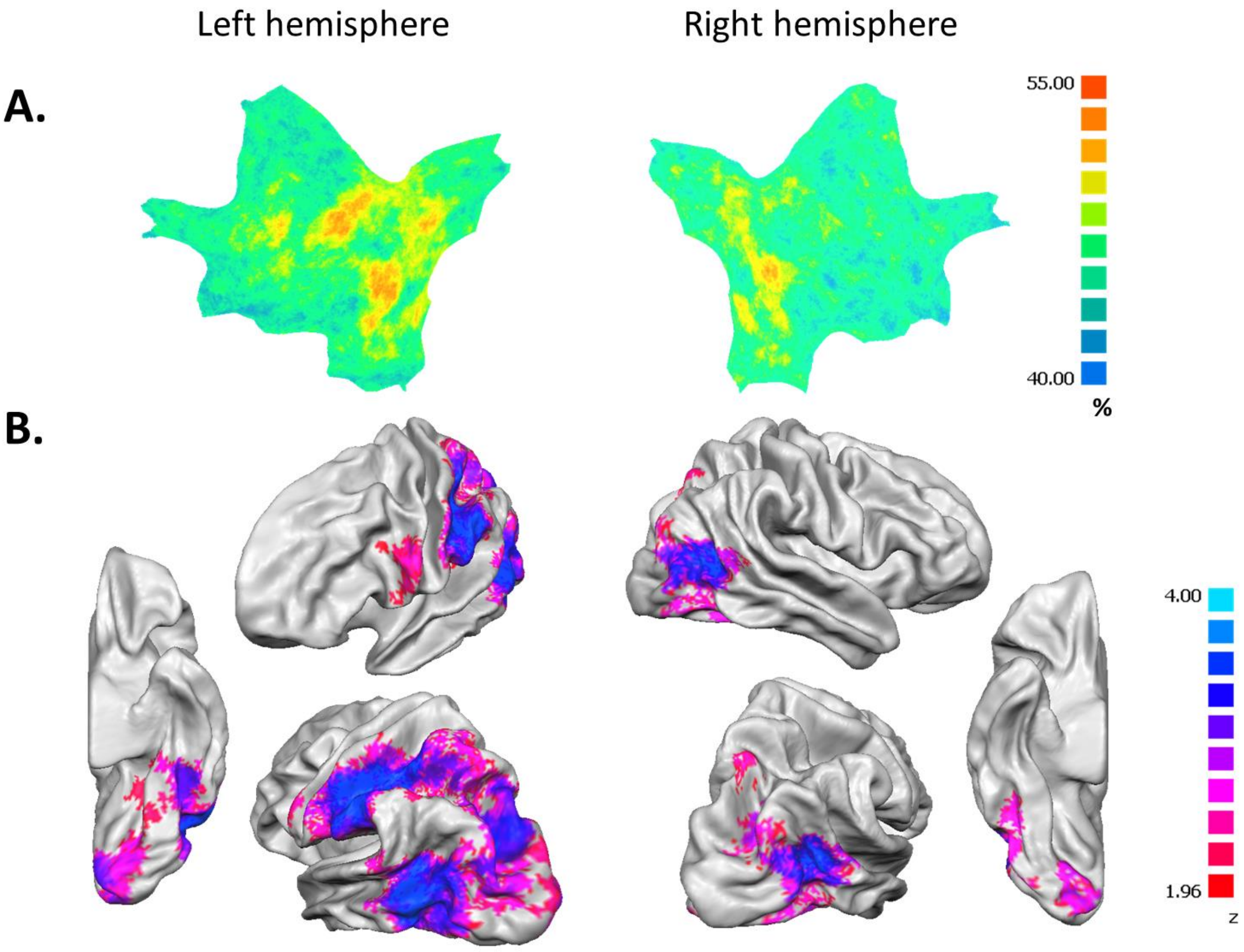

Figure 4.2: Multivariate results. Decoding of transitive and intransitive verbs. A. Mean accuracy maps of the searchlight MVPA. Individual accuracy maps (n = 20) were averaged and projected onto flattened group-averaged hemispheric surfaces. Decoding accuracy at chance is 50%. B. Statistical group maps, corrected using TFCE at α = .05 (two-tailed).

4. Discussion

Argument structure is one of the key aspects of verb processing. It encodes the core participants of an action – the actor himself and, if the action has a goal, the undergoer[25]. It represents an

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[25] We will briefly note here that while most intransitive verbs represent actions performed by a volitional agent (unergative verbs, such as *run*, *talk, dance*), others take an argument that denotes a passive undergoer of an event (unaccusative verbs, such as *fall*, *sleep*, *blush*). Although unaccusativity is known to contribute to the complexity of

important aspect of verb semantics and, at the same time, encodes the syntactic frame on which the sentence is built. Thus, it seems reasonable to assume that the more participants the action involves and the more complex the argument structure of the corresponding verb, the greater the processing load placed on the cognitive system.

Although we predicted that RTs for transitive verbs would be slower than for intransitive ones, the observed difference between naming latencies in the two conditions was very small (25 ± 20 ms) and did not reach statistical significance. While den Ouden et al. (2009) did not provide naming latency data against which we could compare our results, findings of the studies that employed a lexical decision task are highly inconsistent: e.g., whereas Rodríguez-Ferreiro et al. (2014), as expected, found that transitive verbs were processed slower than intransitive ones, Thompson et al. (2007), surprisingly, reported the opposite effect; finally, Thompson et al. (2010) did not observe a significant difference between the conditions. While we do not have a ready explanation for such a discrepancy in the results, the lack of significant difference in RTs reinforces the validity of our neuroimaging findings, as unequal response times could have potentially confounded the results, due to the fact that increased duration of stimulation can increase the net BOLD response (Kable et al., 2004; Taylor, 2014).

The results of the fMRI experiment demonstrated that, in line with our predictions, a number of areas were more strongly activated during naming of transitive than intransitive verbs, suggesting that the information about a verb's argument structure can be accessed already at the level of single-word processing. These results corroborate recent neuroimaging findings (den Ouden et al., 2009; Thompson et al., 2007, 2010; Meltzer-Asscher et al., 2015), as well as reports on patients (Kim & Thompson, 2000; Collina et al., 2001). From the theoretical perspective, our results seem to speak in favor of the lexicalist view, according to which at least some aspects of the argument structure are retrieved already at the lexical level (Jackendoff, 1972; Horvath & Siloni, 2011), rather than being activated at a later, sentential processing stage (Borer, 2005). Yet, some of our findings could also be interpreted in terms of perceptual and conceptual differences

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verb processing, potentially due to the underlying syntactic transformations required to process unaccusative sentences (Shetreet et al., 2010a; Meltzer-Asscher et al., 2015), this subject is beyond the scope of the present study.

between the two subsets of action stimuli rather than in terms of specific linguistic demands. Below we will address some of these possibilities.

The involvement of the left posterior IFG/precentral gyrus in processing of transitivity in our study is in agreement with a previous report by den Ouden et al. (2009) who found that activation in this area increased with the number of thematic roles required by the verb. Interestingly, whereas activation in Broca's area was found in picture naming (den Ouden et al., 2009 and our study), it was not observed during lexical decision (Thompson et al., 2007, 2010). The fact that transitivity-related increase of activity is observed in Broca's area during word production, but not comprehension, may reflect initial phrase structure building (Grewe et al., 2005; Friederici, 2011) — a processing stage that is activated selectively during verb and sentence production, but is not required for passive reading and listening. Supporting evidence for this view comes from agrammatic speakers suffering from damage to the left frontal regions, who show spared verb comprehension, irrespective of the number of thematic roles a verb assigns, but are impaired on verb production (Kim & Thompson, 2000, 2004; Thompson et al., 2012).

The activations in the bilateral middle occipital gyrus (MOG), extending into the posterior middle temporal gyrus (pMTG) in the left hemisphere, corroborate previous reports that implicated the (mainly left) posterior perisylvian cortex in processing of thematic verb structure. Activations in these areas were observed during both verb comprehension (Thompson et al., 2007, 2010; Meltzer-Asscher et al., 2015) and verb production (den Ouden et al., 2009). The role of this region in the retrieval of argument structure is in agreement with the speech comprehension model proposed by Friederici (2012). Whether this activation pertains to exclusively linguistic processes, however, is questionable. As discussed in Section 4.2 of Chapter 3, lateral occipitotemporal cortices are engaged in different aspects of action processing and in encoding various types of action-related information. Since some of the transitive actions in our stimulus set required tool use (*stirare* 'to iron', *saldare* 'to weld', *pelare* 'to peel' etc.), activation of this area, repeatedly implied in tool viewing (Chao et al., 1999; Bracci et al., 2012) is not surprising.

We also found greater activation to transitive than to intransitive verbs in the intraparietal sulcus (IPS), along with the adjacent portions of the superior and inferior parietal lobules. Activation in these areas was also expected. The fact that they were more active during viewing and naming of actions directed at objects and/or required tool use is consistent with data showing that posterior parietal cortices are relevant in goal-directed action and in the representation of tools (for reviews, see Culham & Valyear, 2006; Lewis, 2006).

The most surprising (non-)result of our study is the lack of activations in the left angular/supramarginal gyrus, consistently reported in previous investigations (Thompson et al., 2007, 2010; den Ouden et al., 2009)[26]. According to Thompson and colleagues, these regions may be crucial for the retrieval of information pertaining to the number of thematic roles (for review, see Thompson & Meltzer-Asscher, 2014). Our results are more in line with an alternative account, proposed by Kemmerer (2015). According to this author, the transitivity effects observed in the temporoparietal junction (TPJ) might be driven not by differences in argument structure complexity *per se*, but rather by the semantic reversibility of the actions denoted by verbs. This explanation is consistent with the Theory of Mind framework, according to which the TPJ plays a crucial role in the cognitive ability to understand others as intentional agents (Saxe & Kanwisher, 2003). With respect to its role in processing semantically reversible actions (such as *hug* or *hit*), activation in the TPJ may reflect the subject's effort to understand the causal relations between the core participants of an action ("who acts upon whom?"). On this view, the discrepancy between our results and those obtained by den Ouden et al. (2009) on a similar task could be potentially attributed to the semantic reversibility of verbs. While the majority of transitive actions (7/10) presented in den Ouden et al.'s experiment were directed at people, only one of our drawings (1/18) depicted two people involved in an action (*comb*) and, thus, required disambiguating the roles of the two participants. However, the possibility that the lack of effect in the TPJ in our study results from a type II error ("false negative") cannot be ruled out with certainty. Thus, further research should directly address the effect of semantic reversibility and its potential interaction with transitivity.

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[26] On the contrary, increased activation in the homologous regions of the right hemisphere was observed for intransitive as compared to transitive verbs in our experiment. We do not have a ready explanation for this finding.

Chapter 5. General discussion and future directions

The experimental studies described in this thesis have tackled questions pertaining to the organization of word knowledge in the brain and to the neural correlates of practicing this knowledge.

In the first experiment (Chapter 3) we investigated the differences between the two cross-linguistically most prominent word classes — nouns and verbs — using a picture naming task. Our findings largely corroborate previous reports. They suggest that, while object and action naming is supported by similar cortical networks, verb production results in more intense BOLD signal activation in bilateral lateral occipitotemporal cortices and in predominantly left-lateralized posterior parietal and inferior frontal regions, perhaps due the greater cognitive load imposed by verbs. Although we used the terms “noun”/”object” and “verb”/”action” interchangeably throughout the text, we should note that in the context of a picture naming task it is not possible to reliably establish whether observed distinctions were associated with grammatical or semantic differences between the two word classes. However, given that the target words were produced in a morphologically non-marked form (verbs in the infinitive, nouns in the singular, and without an article), morphosyntactic demands were minimal. Therefore, it is reasonable to hypothesize that different BOLD activations mostly resulted from different conceptual properties of the object and action stimuli (and that verb-selective activity in the left inferior frontal cortex likely reflects greater lexical selection demands). Our assumption is backed up by extant research on the processing of object and action concepts. Recent neuroimaging results suggest that, while the representations of object properties and/or categories are scattered along the ventral occipitotemporal cortices, various aspects of actions are represented in lateral occipitotemporal and parietal regions, potentially in concert with the prefrontal cortex (although whether the latter plays a crucial role in the process is still a matter of debate).

We should note here that while studies on the neurofunctional mechanisms underlying word production and conceptual representations abound, the two lines of research have progressed mainly in parallel, and have rarely relied on each other’s finding when interpreting the results (for a similar argument, see Francis, 2014). That is, while neuroscientists mapping cortical representations of objects and actions pay great attention to various dimensions of perceptual and conceptual processing, they often neglect the "labels" these concepts have in language. At the same time, neurolinguists aiming to tease apart various stages of word processing with the aid of neuroimaging tools are often too quick to ascribe the active areas to purely linguistic functions/properties, without considering alternative explanations in terms of perceptual and conceptual processing.

This state of affairs is unfortunate, as the two fields have a lot to offer to each other.

The importance of considering the findings outside of the language domain when interpreting studies on language can be illustrated by the results of the two experiments we conducted. Interestingly, the effects of transitivity (transitive verbs > intransitive verbs; Fig. 4.1 and 4.2) and word class (verbs > nouns; Fig. 3.7 and 3.10) overlapped to a large degree. Namely, significantly different activations in both cases were observed in the lateral occipitotemporal cortices bilaterally and in the (mostly) left posterior parietal cortices, as well as in the left posterior inferior frontal cortex/precentral gyrus. While these areas have been previously implicated in preferential processing of verbs over nouns and of transitive over intransitive verbs in the neurolinguistic literature, we argue that, in accordance with the Occam's razor principle, a more parsimonious explanation providing a common account for both phenomena would be preferable. Indeed, as discussed in the previous chapters, some of the observed activation differences between the two conditions in both experiments could be attributed to perceptual and conceptual properties of the stimuli, such as visual complexity, instrumentality, etc.

To give another example, the temporoparietal junction (TPJ), extending from the posterior superior temporal sulcus (pSTS) to the angular gyrus, that has been implicated in processing of action concepts (Lingnau & Downing, 2015; Culham & Valyear, 2006) and thematic role assignment (Thompson & Meltzer-Asscher, 2014), has also been reported to be involved in processing of biological motion (Puce & Perrett, 2003), animacy of event participants (Grewe et al., 2007), semantic reversibility of actions (Thothathiri et al., 2012), theory of mind (Saxe & Kanwisher, 2003), agency detection and intentionality (Castelli et al., 2000; Osaka et al., 2012). The overarching theme of all these findings is the representation of energy flow and forcedynamic causal relations (Kemmerer, 2015, 2014). Thus, it is possible that activation in the temporoparietal junction across various tasks and domains pertains to the same underlying cognitive process (for a compatible view of the pSTS function, see Hein & Knight, 2008). This hypothesis is indirectly corroborated by the observation that TPJ is recruited during processing of transitivity to a greater degree if the two participants of an action are animate, and the direction of "energy flow" requires disambiguation. Future experiments comparing transitive actions directed at people and at inanimate objects could help confirm or refute this conjecture.

On the other hand, discoveries in the field of theoretical linguistics can assist in the advancement of neuroscience. Kemmerer (2014) provides an example of how insights from lexical semantics could help us gain a better understanding of the cognitive bases of argument structure. While several recent fMRI findings have focused on the neural correlates of transitive and intransitive verbs (for a short review, see Chapter 4), the observed activation differences between the two types of verbs may be driven by more subtle lexical-semantic distinctions, which are well known in theoretical linguistics. For example, while verbs denoting "hitting" (*hit*, *slap*, *poke*, etc.), "cutting" (*cut*, *scratch*, *slice*, etc.) and "breaking" (*break*, *shatter*, *chip*, etc.) exhibit superficially similar behavior, as they are all transitive and are used in similar constructions (X_{ACTOR} hits/cuts/breaks $Y_{\text{UNDERGOER}}$), on closer inspection they reveal different distributional properties which are rooted in their semantics. Namely, the meaning of these verbs could be decomposed into two semantic components, "CONTACT" and "CHANGE OF STATE" (Fillmore, 1970; Levin, 1993). While "hitting" requires physical contact of the actor with the undergoer, it does not entail the change of state of the latter. On the contrary, "breaking" does not necessarily require the actor and the undergoer to get into physical contact, but causes a change of state of the undergoer. "Cutting", in turn, implies both contact and change of state. These seemingly minor semantic differences have implications for distributional properties of the verbs, i.e., they restrict the types of grammatical constructions in which they can be used[27]. "CONTACT" is the prerequisite for possessor raising, in which acting on an object is reconceptualized as acting on its

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[27] The examples provided below are borrowed from Kemmerer (2014). Here we use the commonly accepted linguistic notation, in which grammatically correct expressions are preceded by ^{OK}, and non-grammatical structures are marked with an asterisk (*).

possessor (e.g., *I hit/cut Brian's arm* → ^{OK}*I hit/cut Brian on the arm*; but ^{OK}*I broke Brian's arm* → **I broke Brian on the arm*). "CHANGE OF STATE" is a necessary condition for the verb to be used in so-called 'middle constructions', i.e., sentences in which the undergoer, typically denoted by an object of a two-argument predicate, is raised to the subject position of a one-argument predicate to convey the meaning of generic property/proneness of the undergoer to change its state (*I cut/broke the glass.* → ^{OK}*Glass cuts/breaks easily*; but *I hit the wall* → **The wall hits easily*). Finally, "CHANGE OF STATE" in the absence of "CONTACT" is the prerequisite of forming inchoative constructions, in which the undergoer is raised to a subject position of an intransitive sentence to convey the meaning of transformation, without an explicit mention of the cause of this transformation (*I broke the computer* → ^{OK}*The computer broke*; but *I hit the car* → **The car hit, I cut the rope* → **The rope cut*).

It seems plausible that semantic parameters, such as "CHANGE OF STATE" and "CONTACT", that are sufficiently relevant from the cognitive perspective as to affect the distributional properties of the verbs, may have separable neural representations. Indeed, a recent fMRI study by Kemmerer et al. (2008) showed that these sets of verbs are processed by partially segregated neural networks. Thus, balancing stimuli for these parameters is important when investigating the neural correlates of transitivity.

As the reader may have noticed, the middle and inchoative syntactic transformations, described above, essentially transform the transitive (two-argument) verb into an intransitive (one-argument) one. The ability of verbs to take on a different number of arguments has been recently scrutinized by neurolinguists (Shetreet et al., 2007; Meltzer-Asscher et al., 2013). In these studies, verbs with alternating transitivity (i.e., verbs that can be used both transitively and intransitively) recruit to a greater degree a number of regions, including portions of the temporoparietal junction and the middle/superior frontal gyrus. While the authors explained these findings in terms of greater cognitive load placed by alternating verbs due to simultaneous activation of two possible thematic grids and processing of lexical ambiguity, it cannot be ruled out that at least some of the activation differences are due to lexical-semantic factors.

Another aspect of argument structure we only briefly touched upon in Chapter 4 is the division of intransitive verbs into unergative (denoting actions performed by a volitional agent, e.g. *Mary combs her hair*) and unaccusative (predicating events happening to a passive undergoer, e.g., *Johnny sleeps*). Unaccusative predicates are less common in language and pose a greater problem for aphasic speakers (Kegl, 1995; Thompson, 2003; Bastiaanse & van Zonneveld, 2005; Lee & Thompson, 2004, 2011). Neuroimaging evidence suggests that they are also processed differently by healthy subjects (Lee & Thompson, 2011; Shetreet et al., 2010a). The above-mentioned studies almost univocally attributed the increased cognitive demands posed by unaccusativity to the underlying syntactic transformations raising the undergoer to the position of the subject, which is predicted by generative grammar theories. However, as argued by Kemmerer (2014), the observed distinction between unaccusative and unergative verbs could also be explained by subtle semantic distinctions, and the clues about such distinctions could be found in the extant literature generated by decades of research in the field of lexical and semantic typology.

The second question addressed by our study pertained to the effects of practicing lexical knowledge in healthy subjects. Previous findings indicated that practiced naming is associated with significant activation changes in a number of brain areas. Following the suggestion of Nickels (2002) and Heath et al. (2015), we proposed that the changes associated with practice in the healthy brain could be potentially useful for interpreting the studies focusing on functional plasticity in anomic subjects undergoing naming treatment. While functional reorganization following brain damage is an overwhelmingly complex phenomenon, to which both lesion (size and location, amount of damage to grey and white matter) and patient (e.g., age, education, handedness) characteristics contribute, establishing the baseline of the mechanisms underlying word practice in the cognitively healthy individual is a necessary first step in pinpointing the areas that could serve as predictors of naming improvement in patients. We found that the neural loci of intensive training of nouns and verbs were separable from priming effects resulting from a single stimulus repetition, two weeks after the initial exposure. Namely, a ten-day practice of words belonging to both grammatical classes was associated with a similar set of BOLD activation changes, encompassing both the classic language network and areas that are typically considered domain-general. Interestingly, training-related changes in BOLD amplitude had a contrasting direction in different areas. Whereas the left anterior brain regions (posterior inferior frontal cortex, anterior insula, anterior cingulate cortex) exhibited decreased activity, the BOLD response in the left posterior regions (precuneus, posterior cingulate cortex, angular gyrus, posterior middle temporal gyrus) was increased.

Our results map well onto those obtained by Fridriksson (2010) in individuals suffering from anomia. Nineteen patients with left-hemispheric stroke and chronic aphasia[28] underwent two weeks of intensive naming therapy and were scanned before and after the treatment protocol. At a group level, fMRI analysis revealed a positive relationship between treatment-induced naming improvement and modulation of activity in both the anterior (pars opercularis, precentral gyrus, middle frontal gyrus) and posterior (precuneus, inferior parietal lobule, superior parietal lobule) regions of the left hemisphere[29]. Of particular interest here is the finding of practice-induced modulation in the parietal cortices that are traditionally considered domain-general. Although functional changes in these regions did not receive much attention in the clinical literature that prefers to focus on the perisylvian areas and their right-hemispheric homologues, some recent reports suggested involvement of the parietal areas (and, in particular, precuneus) in naming improvement. According to these reports, “cortical areas not traditionally related to language processing may support anomia recovery in some patients with chronic aphasia” (Fridriksson et al., 2007), thus, “functional integrity of domain-unspecific memory structures may be a prerequisite for successful (intensive) language interventions” (Menke et al., 2009). Our “treatment simulation” study with healthy adults identified the areas in the medial and lateral parietal cortex that are potentially subserving the retrieval of knowledge about trained items from long-term memory. The intactness and potential functional reorganization of these areas following practice should be accounted for in naming treatment studies with patients.

Assuming that deactivations/inactivations of different brain areas pertain to facilitation at different levels of stimulus processing, we have tried to provide an account for a potential role of

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[28] As expected in a heterogeneous sample of stroke patients with different lesion locations and sizes, the nature and extent of the observed speech deficits varied considerably.

[29] Note, however, that patients in (Fridriksson, 2010) showed upregulation in both anterior and posterior regions following treatment.

each of the active clusters in practice by relying on “reverse inferences”, i.e., by discussing which functions these regions are commonly associated with in the neuroimaging literature. Another interesting approach, however, is to consider the observed changes as a whole, and to interpret them in terms of functional modulation of activity in large-scale brain networks, including the executive, salience (Bressler & Menon, 2010) and default mode (Buckner et al., 2008) networks. The neuroimaging community has recently shifted from a strictly modular approach, that attributes a separate function (or set of functions) to each brain region, to one that focuses on the interaction between different brain regions working in concert during task performance. This novel approach offers a promising tool, which could potentially allow a better understanding of the complex workings of the human mind. Thus, future studies of training could greatly benefit not only from measuring activation changes associated with practice, but also from gathering additional information about the functional and structural connectivity of the regions in which these changes are observed.

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APPENDICES

Appendix A. Stimulus list of the training study (Chapter 3)

Italian word	English translation	Rel. frequency	# syllables	# phonemes	Vis. complex. (obj.)	Vis. complex. (subj.)	PNA	AoA	Familiarity	Imageability
TRAINED NOUNS (condition "NT")										
pompiere	fireman	4,25	3	8	35	3,24	100	2,29	2,93	4,63
scoiattolo	squirrel	0,62	4	10	25	2,88	100	1,84	2,92	4,63
tartaruga	turtle	2,28	4	9	40	3,02	93,8	1,65	3,25	4,84
pappagallo	parrot	1,61	4	10	40	3,06	91,7	1,76	2,88	4,71
trifoglio	shamrock	0,06	3	8	32	1,56	87,5	2,73	2,55	4,32
ananas	pineapple	0,8	3	6	44	2,3	100	2,29	3,62	4,74
faro	lighthouse	6,03	2	4	41	2,06	100	2,67	2,7	4,55
lampadario	chandelier	0,72	4	10	58	3,62	91,7	2,24	3,7	4,34
culla	cradle	6,24	2	5	76	3,16	91,7	1,51	2,93	4,79
sveglia	alarm clock	2,58	2	6	41	1,76	100	1,96	4,78	4,63
altalena	swing	2,97	4	8	51	1,82	100	1,65	3,13	4,57
grembiule	apron	2,22	3	9	37	2,04	100	1,93	3,1	4,5
manichino	dummy	0,97	4	8	16	2,12	87,5	3,18	3,13	4,19
batteria	drum set	10,55	4	8	62	3,12	100	2,53	4,18	4,16
mongolfiera	air balloon	0,33	4	11	52	2,3	100	2,56	2,37	4,47
aquilone	kite	0,63	4	8	20	1,52	100	2,07	2,42	4,7
ombrello	umbrella	5,07	3	8	15	1,56	97,9	1,67	4,27	4,87
ventilatore	fan	1,2	5	11	44	2,92	100	2,49	4,18	4,54
cannone	cannon	6,98	3	7	62	3	100	2,82	2,92	4,45
serratura	door lock	2,64	4	9	36	2,32	89,6	2,65	3,47	4,45
MEAN		*2,94*	*3,45*	*8,15*	*41,35*	*2,47*	*96,57*	*2,22*	*3,27*	*4,55*
SD		*2,77*	*0,83*	*1,87*	*15,88*	*0,66*	*4,78*	*0,47*	*0,66*	*0,2*

Italian word	English translation	Rel. frequency	# syllables	# phonemes	Vis. complex. (obj.)	Vis. complex. (subj.)	PNA	AoA	Familiarity	Imageability
UNTRAINED NOUNS (condition "NU")										
cameriere	waiter	9,04	4	9	37	3	97,9	2,15	4,27	4,63
pinguino	penguin	0,38	3	8	20	2,42	100	1,82	2,98	4,76
coccodrillo	crocodile	2,26	4	11	49	3,64	93,8	1,71	2,57	4,54
struzzo	ostrich	1,31	2	8	29	3,22	95,8	2,35	2,55	4,53
cactus	cactus	1,11	2	6	42	2,42	100	2,84	2,82	4,58
zucca	pumpkin	5,27	2	6	65	1,9	100	2,02	3,1	4,68
mulino	mill	2,89	3	6	66	3,64	87,5	2,51	2,87	4,42
cassaforte	safe	5,6	4	10	41	3,4	97,9	2,96	2,77	4,05
materasso	mattress	5,01	4	9	49	1,34	100	2,05	3,75	4,58
bussola	compass	2,28	3	7	58	2,9	100	2,53	2,73	4,61
slitta	sledge	0,98	2	6	31	1,96	100	2,4	2,22	4,32
reggiseno	bra	1,45	4	10	54	2,44	97,9	3,25	4,47	4,61
semaforo	traffic lights	6,71	4	8	34	3,4	100	2,33	4,5	4,79
tromba	trumpet	4,5	2	6	30	2,78	95,8	2,31	3,23	4,55
sottomarino	submarine	1,15	5	11	52	3,28	91,7	2,95	2,17	4
estintore	fire extinguisher	0,62	4	9	26	2,2	95,8	3,25	2,65	4,35
racchetta	racket	4,13	3	8	32	1,7	97,9	2,36	2,87	4,51
tavolozza	palette	0,61	4	10	37	2,26	87,5	3,02	2,2	4,45
camino	fireplace	4,87	3	6	61	2,34	100	2,09	3,17	4,5
clessidra	hourglass	0,01	3	9	53	2,08	100	3,04	2,37	4,39
MEAN		*3*	*3,25*	*8,15*	*43,3*	*2,62*	*96,98*	*2,5*	*3,01*	*4,5*
SD		*2,49*	*0,91*	*1,76*	*13,65*	*0,67*	*4,02*	*0,47*	*0,71*	*0,2*

Italian word	English translation	Rel. frequency	# syllables	# phonemes	Vis. complex. (obj.)	Vis. complex. (subj.)	PNA	AoA	Familiarity	Imageability
TRAINED VERBS (condition "VT")										
belare	bleat	0,4	3	6	20	2,06	100	2,82	1,82	3,41
sciare	ski	2,46	3	5	33	3,86	100	2,35	2,83	4,62
abbaiare	bark	1,55	4	8	16	2,02	97,9	1,65	3,78	4,49
covare	hatch (eggs)	2,88	3	6	47	3,28	95,8	2,4	2,67	3,97
sventolare	wave (flag)	4,96	4	10	31	2,4	100	2,67	3,35	4,41
starnutire	sneeze	0,53	4	10	40	3,5	87,5	1,91	4,17	4,65
fischiare	blow (whistle)	6,17	3	8	39	3,18	100	1,89	3,97	4,62
remare	row (boat)	0,98	3	6	45	3,7	95,8	2,53	2,47	4,54
navigare	sail (yacht)	9,21	4	8	53	2,58	89,6	2,45	3,2	4,03
cucire	sew (dress)	7	3	7	54	3,46	95,8	2,22	3,32	4,59
leccare	lick (ice-cream)	2,22	3	7	36	2,4	100	1,67	3,87	4,68
pungere	sting (arm)	3,63	3	8	31	3,06	87,5	1,75	3,87	4,27
inzuppare	dip (cookie)	0,29	4	10	56	3,24	68,8	2,4	3,28	4,41
impastare	knead (dough)	2,4	4	9	54	2,94	97,9	2,47	3,3	4,46
tosare	shear (sheep)	0	3	6	56	3,74	95,8	3,09	2,28	3,92
timbrare	stamp (letter)	0,98	3	8	37	3,74	97,9	2,93	3,03	4,41
incollare	glue (vase)	3,87	4	9	28	3,48	68,9	1,93	3,52	4,38
marciare	march	9,41	3	8	89	3,98	100	3	2,45	4,41
miagolare	meow	0,23	4	9	30	2,16	100	1,69	3,38	4,38
grattuggiare	grate (cheese)	2,29	4	10	58	3,78	95,8	2,44	3,77	4,43
MEAN		*3,07*	*3,45*	*7,9*	*42,65*	*3,13*	*93,75*	*2,31*	*3,22*	*4,35*
SD		*2,9*	*0,51*	*1,55*	*16,53*	*0,64*	*9,41*	*0,46*	*0,63*	*0,31*

Italian word	English translation	Rel. frequency	# syllables	# phonemes	Vis. complex. (obj.)	Vis. complex. (subj.)	PNA	AoA	Familiarity	Imageability
UNTRAINED VERBS (condition "VU")										
sputare	spit	3,64	3	7	15	2,82	100	1,95	3,23	4,51
spalmare	spread (butter)	2,85	3	8	55	2,96	87,5	2,16	3,63	4,65
beccare	peck (person)	5,22	3	7	35	3,8	83,3	2,24	3,27	4,05
sbadigliare	yawn	0,55	4	10	48	3,44	97,9	1,84	4,3	4,78
innaffiare	water (flower)	2,74	4	10	41	3,1	97,9	2,2	3,52	4,49
saldare	weld (metal)	7,37	3	7	43	3,72	93,8	3,58	2,62	3,38
pattinare	ice-skate	0,42	4	8	45	3,42	100	2,4	2,52	4,46
nuotare	swim	10,86	3	7	49	3,7	100	1,73	3,82	4,76
annusare	sniff (flower)	3,53	4	8	41	3,12	89,6	2,07	3,62	4,51
gattonare	crawl	0	4	9	36	2,78	97,9	1,98	2,48	4,54
tossire	cough	1,58	3	7	41	3,6	79,2	1,73	3,9	4,51
stirare	iron (shirt)	3,11	3	7	58	3,7	100	2,27	3,77	4,65
pettinare	comb (hair)	1,38	4	9	34	3,56	89,6	1,73	4,2	4,73
spremere	squeeze (lemon)	4,2	3	8	24	3,14	100	2,25	3,28	4,43
pelare	peel (potatoes)	1,13	3	6	65	3,62	100	2,85	3,5	4,24
mungere	milk (cow)	0,41	3	8	45	3,54	100	2,38	2,37	4,27
martellare	hammer (nail)	1,63	4	10	61	3,28	95,6	2,78	2,65	4,38
decollare	take off	7,03	4	9	45	2,8	66,7	3,09	2,85	4,46
muggire	moo	0,23	3	8	26	2,64	95,8	2,4	2,07	4,03
ruggire	roar	1	3	8	39	3,2	100	2,24	2,2	3,95
MEAN		*2,94*	*3,4*	*8,05*	*42,3*	*3,3*	*93,74*	*2,3*	*3,19*	*4,39*
SD		*2,85*	*0,5*	*1,15*	*12,35*	*0,36*	*8,88*	*0,48*	*0,68*	*0,33*

Parameters for which the four subsets of stimuli were matched:

Rel. frequency	relative frequency of a lemma obtained from the online database of written Italian language *Corpus e Lessico di Frequenza dell'Italiano Scritto* (CoLFIS; Bertinetto et al., 2005); http://esploracolfis.sns.it/EsploraCoLFIS/#!0:t=L
# syllables and **# phonemes**	phonemic and syllabic length of a word (including inflection markers)
Vis. complex. (obj.)	objective visual complexity score calculated as the size of an image file after GIF compression (Forsythe et al., 2008)
Vis. complex. (subj.)	subjective visual complexity, calculated as a mean rating given to a word by participants of an online questionnaire (n = 50); note that this was the only dimension on which we were not able to match the subsets of stimuli, due to the fact that verbs were deemed significantly more complex than nouns
PNA	picture-name agreement score obtained from an online questionnaire (n = 48), measured as the percentage of target responses to a word; close synonyms were accepted and were counted as one nomination with the target word, on condition that they had similar usage frequencies
AoA	subjective age of acquisition rating obtained from an online questionnaire (n = 55)
Familiarity	subjective familiarity rating obtained from an online questionnaire (n = 60)
Imageability	imageability rating obtained from an online questionnaire (n = 38)

The output of non-parametric Kruskal-Wallis tests (one-way ANOVA on ranks) assessing the differences between the four stimulus subsets on a number of parameters:

	Mean(SD)				**Kruskal-Wallis test results**	
	NT	NU	VT	VU	$\chi^2(3)$	*p*
Rel. frequency	2,94(2,77)	3,0(2,49)	3,07(2,9)	2,94(2,85)	0,006	0,996
# syllables	3,45(0,83)	3,25(0,91)	3,45(0,51)	3,4(0,5)	0,804	0,848
# phonemes	8,15(1,57)	8,15(1,76)	7,9(1,55)	8,05(1,15)	0,43	0,934
Vis. complex. (obj.)	41,35(15,88)	43,3(13,65)	42,65(16,53)	42,3(12,35)	0,245	0,97
Vis. complex. (subj.)	2,47(0,66)	2,62(0,67)	3,13(0,64)	3,3(0,36)	20,169	**< 0,001**
PNA	96,57(4,78)	96,98(4,02)	93,75(9,4)	93,74(8,88)	2,158	0,54
AoA	2,22(0,47)	2,5(0,47)	2,31(0,46)	2,29(0,48)	3,473	0,324
Familiarity	3,27(0,66)	3,01(0,71)	3,22(0,63)	3,19(0,68)	2,629	0,452
Imageability	4,55(0,2)	4,49(0,2)	4,35(0,31)	4,39(0,33)	6,549	0,088

As evidenced by the results of the statistical tests, differences between the four subsets were not statistically significant for all parameters, with the exception of subjective visual complexity ($p < .001$). The raters on this test considered action drawings significantly more complex that object drawings. The effect of imageability also showed a trend for significance ($p = .088$), with nouns consistently rated as more imageable than verbs.

Appendix B. *F*-statistics and *p*-values for training, word class effects and their interaction in 10 ROIs (Chapter 3)

Results of the two-way repeated measures ANOVA with within-subject factors word class (nouns, verbs) and training (untrained, trained) in 10 left-hemispheric spherical ROIs are summarized in the table below. Results that are statistically significant at α = .05 are indicated **in bold**.

ROI	**Talairach center coordinates (x, y, z)**	**word class effect**			**training effect**			**word class × training interaction**		
		F(1, 19)	*p*, uncorr.	p_{FDR}	*F*(1, 19)	*p*, uncorr.	p_{FDR}	*F*(1, 19)	*p*, uncorr.	p_{FDR}
pars orbitalis	(-36, 27, -5)	0,315	0,581	0,67	3,965	0,061	0,183	0,352	0,56	0,672
pars triangularis	(-41, 17, 6)	2,071	0,166	0,332	16,718	**0,001**	**0,03**	< 0,001	0,986	0,986
pars opercularis	(-52, 10, 20)	13,132	**0,002**	**0,03**	7,352	**0,014**	**0,053**	0,634	0,436	0,623
ACC	(-1.9, 13, 41)	3,44	0,079	0,216	7,932	**0,011**	**0,047**	0,064	0,803	0,831
postITG	(-44, -59, -7)	9,28	**0,007**	**0,042**	0,55	0,468	0,61	0,127	0,726	0,778
midMTG	(-55, -37, 5)	9,097	**0,007**	**0,035**	4,927	**0,039**	0,13	0,163	0,691	0,768
postSTG	(-48, -38, 14)	2,793	0,111	0,256	2,078	0,166	0,311	0,582	0,455	0,621
extrastriate	(-38, -82, -4)	2,591	0,124	0,266	0,671	0,423	0,668	0,876	0,361	0,602
PCC	(-3.5, -36, 27)	2,027	0,171	0,302	12,149	**0,002**	**0,02**	0,65	0,43	0,645
precuneus	(-4.4, -71, 31)	3,088	0,095	0,238	11,219	**0,003**	**0,023**	0,532	0,475	0,594

ACC = anterior cingulate cortex; postITG = posterior inferior temporal gyrus; midMTG = mid-portion of middle temporal gyrus; postSTG = posterior superior temporal gyrus; PCC = posterior cingulate cortex.

Appendix C. Stimulus list of the transitivity study (Chapter 4)

Italian word	English translation	Rel. frequency	# syllables	# phonemes	Vis. complex. (obj.)	Vis. complex. (subj.)	PNA	AoA	Familiarity	Imageability
INTRANSITIVE VERBS										
belare	bleat	0,4	3	6	20	2,06	100	2,82	1,82	3,41
sciare	ski	2,46	3	5	33	3,86	100	2,35	2,83	4,62
abbaiare	bark	1,55	4	8	16	2,02	97,9	1,65	3,78	4,49
starnutire	sneeze	0,53	4	10	40	3,5	87,5	1,91	4,17	4,65
fischiare	whistle	6,17	3	8	39	3,18	100	1,89	3,97	4,62
remare	row	0,98	3	6	45	3,7	95,8	2,53	2,47	4,54
navigare	sail	9,21	4	8	53	2,58	89,6	2,45	3,2	4,03
marciare	march	9,41	3	8	89	3,98	100	3	2,45	4,41
miagolare	meow	0,23	4	9	30	2,16	100	1,69	3,38	4,38
sputare	spit	3,64	3	7	15	2,82	100	1,95	3,23	4,51
sbadigliare	yawn	0,55	4	10	48	3,44	97,9	1,84	4,3	4,78
pattinare	ice-skate	0,42	4	8	45	3,42	100	2,4	2,52	4,46
nuotare	swim	10,86	3	7	49	3,7	100	1,73	3,82	4,76
gattonare	crawl	0	4	9	36	2,78	97,9	1,98	2,48	4,54
tossire	cough	1,58	3	7	41	3,6	79,2	1,73	3,9	4,51
decollare	take off	7,03	4	9	45	2,8	66,7	3,09	2,85	4,46
muggire	moo	0,23	3	8	26	2,64	95,8	2,4	2,07	4,03
ruggire	roar	1	3	8	39	3,2	100	2,24	2,2	3,95
MEAN		*3,13*	*3,44*	*7,83*	*39,39*	*3,08*	*94,91*	*2,2*	*3,08*	*4,4*
SD		*3,68*	*0,51*	*1,34*	*16,71*	*0,62*	*9,03*	*0,45*	*0,78*	*0,34*

Italian word	English translation	Rel. frequency	# syllables	# phonemes	Vis. complex. (obj.)	Vis. complex. (subj.)	PNA	AoA	Familiarity	Imageability
					TRANSITIVE VERBS					
covare	hatch (eggs)	2,88	3	6	47	3,28	95,8	2,4	2,67	3,97
sventolare	wave (flag)	4,96	4	10	31	2,4	100	2,67	3,35	4,41
leccare	lick (ice-cream)	2,22	3	7	36	2,4	100	1,67	3,87	4,68
pungere	sting (arm)	3,63	3	8	31	3,06	87,5	1,75	3,87	4,27
impastare	knead (dough)	2,4	4	9	54	2,94	97,9	2,47	3,3	4,46
tosare	shear (sheep)	0	3	6	56	3,74	95,8	3,09	2,28	3,92
timbrare	stamp (letter)	0,98	3	8	37	3,74	97,9	2,93	3,03	4,41
grattuggiare	grate (cheese)	2,29	4	10	58	3,78	95,8	2,44	3,77	4,43
beccare	peck (person)	5,22	3	7	35	3,8	83,3	2,24	3,27	4,05
innaffiare	water (flower)	2,74	4	10	41	3,1	97,9	2,2	3,52	4,49
saldare	weld (metal)	7,37	3	7	43	3,72	93,8	3,58	2,62	3,38
annusare	sniff (flower)	3,53	4	8	41	3,12	89,6	2,07	3,62	4,51
stirare	iron (shirt)	3,11	3	7	58	3,7	100	2,27	3,77	4,65
pettinare	comb (hair)	1,38	4	9	34	3,56	89,6	1,73	4,2	4,73
spremere	squeeze (lemon)	4,2	3	8	24	3,14	100	2,25	3,28	4,43
pelare	peel (potatoes)	1,13	3	6	65	3,62	100	2,85	3,5	4,24
mungere	milk (cow)	0,41	3	8	45	3,54	100	2,38	2,37	4,27
martellare	hammer (nail)	1,63	4	10	61	3,28	95,6	2,78	2,65	4,38
MEAN		*2,78*	*3,38*	*8*	*44,28*	*3,33*	*95,58*	*2,43*	*3,27*	*4,32*
SD		*1,85*	*0,5*	*1,41*	*11,94*	*0,44*	*5*	*0,5*	*0,56*	*0,32*

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