A right visual field advantage for visual processing of manipulable objects

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Abstract Information about object-associated manipulations is lateralized to left parietal regions, while information about the visual form of tools is represented bilaterally in ventral occipito-temporal cortex. It is unknown how lateralization of motor-relevant information in left-hemisphere dorsal stream regions may affect the visual processing of manipulable objects. We used a lateralized masked priming paradigm to test for a right visual field (RVF) advantage in tool processing.

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Target stimuli were tools and animals, and briefly presented primes were identical to or scrambled versions of the targets. In Experiment 1, primes were presented either to the left or to the right of the centrally presented target, while in Experiment 2, primes were presented in one of eight locations arranged radially around the target. In both experiments, there was a RVF advantage in priming effects for tool but not for animal targets. Control experiments showed that participants were at chance for matching the identity of the lateralized primes in a picture–word matching experiment and also ruled out a general RVF speed-of-processing advantage for tool images. These results indicate that the overrepresentation of tool knowledge in the left hemisphere affects visual object recognition and suggests that interactions between the dorsal and ventral streams occurs during object categorization.

Introduction

An important issue is how basic principles of organization of the primate visual system contribute to determining the cortical organization of object knowledge. The first cortical stage of visual processing in the primate brain processes information from the contralateral visual field: Early visual regions in the left hemisphere process stimuli presented to the right visual field (RVF) across both eyes, and early visual regions in the right hemisphere process stimuli presented to the left visual field (LVF) across both eyes (e.g., Engel, Glover, & Wandell, 1997; Felleman & Van Essen, 1991). Independently of this property of the visual system, some domains of information are lateralized to the left or right hemisphere. For example, language is predominantly left

lateralized in the majority of individuals (e.g., Gazzaniga & Smylie, 1984; Knecht et al., 2000). Investigations of hemispheric biases in visual processing of different classes of stimuli have found visual field advantages contralateral to the hemisphere that differentially represents that domain. For instance, there is a strong RVF advantage for recognition of printed words (e.g., Bub & Lewine, 1988; Finkbeiner, Almeida, & Caramazza, 2006; Hunter & Brysbaert, 2008). Knowledge about how to manipulate objects is also strongly left lateralized in the majority of individuals (Johnson-Frey, 2004; Kroliczak & Frey, 2009). The goal of the present investigation was to test the hypothesis that the overrepresentation of tool knowledge in the left hemisphere leads to a RVF advantage for visual processing of tool stimuli.

A second principle of organization within the primate visual system that is relevant to understanding hemispheric lateralization of tools is the division of labor between the dorsal and ventral visual pathways. The dorsal visual pathway projects from V1 to dorsal occipital cortex and posterior parietal cortex, while the ventral stream projects from V1 to ventral and lateral occipito-temporal regions, terminating in anterior temporal cortex (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991; Ungerleider & Mishkin, 1982; see also Goodale, Kroliczak, & Westwood, 2005; Ungerleider, 1995). The classic understanding of the division of labor between these two streams is that the dorsal stream is critical for extracting visuomotor and spatial information relevant to action, while the ventral stream extracts object identity across variations in size, orientation, luminance, and distance.

Functional magnetic resonance imaging (fMRI) studies indicate that tool knowledge is strongly left lateralized in the dorsal stream, but not in the ventral stream. Specifically, viewing tools, as compared with a baseline category such as animals, elicits differential BOLD responses in the left ventral premotor cortex, the left inferior parietal lobule, and the left middle temporal gyrus, while the same contrast leads to differential activation bilaterally in the medial fusiform gyrus in the ventral stream (Chao & Martin, 2000; Mahon et al., 2007; Noppeney, Price, Penny, & Friston, 2006; for reviews, see Lewis, 2006; Martin, 2007).

Other functional imaging studies have further decomposed the function of the brain regions that make up the tool network. For instance, Kellenbach, Brett, and Patterson (2003) identified regions in the left posterior parietal cortex, left ventral premotor cortex, and left posterior middle temporal gyrus that were activated when participants made decisions about the motor movements associated with object use (see also Boronat et al., 2005). Canessa et al. (2008) replicated the findings of Kellenbach and colleagues and of Boronat and colleagues in left parietal cortex and also found that judgments about object function lead to differential activation near the left temporal pole (see also Anzellotti, Mahon, Schwarzbach, & Caramazza, 2011, for relevant

findings). Those functional imaging data converge with the patterns of impairments observed in brain-damaged patients: Brain damage affecting left-hemisphere parietal structures can lead to impairments for knowledge of how to manipulate tools (Johnson-Frey, 2004; Mahon et al., 2007; Tranel, Damasio, & Damasio, 1997). In contrast, neurological diseases that lead to deterioration of anterior temporal cortices (e.g., semantic dementia, Alzheimer's disease, herpes simplex encephalitis) can be associated with impaired knowledge of object function and spared knowledge of how to manipulate objects (e.g., Negri, Lunardelli, et al., 2007; Sirigu, Duhamel, & Poncet, 1991; but see Hodges, Spatt, & Patterson, 1999). An interesting and currently debated issue is whether the left-lateralized organization of visuomotor knowledge of tools and their action-based properties follows the lateralization of language representations, irrespective of handedness (see, e.g., Kroliczak & Frey, 2009; Kroliczak, Piper, & Frey, 2011; for a review, see Roby-Brami, Hermsdörfer, Roy, & Jacobs, 2012).

There is some indication that the overrepresentation of visuomotor tool knowledge in left dorsal stream regions has behavioral consequences. In a recent bilateral visual field presentation experiment, Verma and Brysbaert (2011) reported that participants were 17 ms faster to recognize tools when the to-be-recognized tool was presented to the RVF; importantly, the RVF advantage was not found in an object/nonobject categorization experiment that presented images in the identical visual field locations (see also Hunter & Brysbaert, 2008, for RVF effects with linguistic stimuli). Handy, Grafton, Shroff, Ketay, and Gazzaniga (2003) used a combination of ERP (Experiment 1 and 2) and fMRI (Experiment 3) to investigate spatial attention for tools; the right visual field, along with the lower visual field, was found to dominantly capture participants' attention (as measured with the contralateral P1 response at lateral occipital recording sites in the ERP experiments). Handy and colleagues argued that the differential P1 activity observed when tools were presented in the lower right visual quadrant reflected the extraction of visuomotor information that implicitly biases attention toward that location. The results from their fMRI experiment suggest that the RVF effects were mediated by left-lateralized parietal and premotor brain regions that process action-related properties of tools.

Thus, on the basis of previous research, there is some indication that tools may enjoy a RVF advantage for visual analysis. Here, we sought to directly evaluate this issue by asking participants to categorize centrally presented images of tools and animals that were immediately preceded by lateralized primes. In Experiment 1, the primes were presented to the left or to the right of the target position. In Experiment 2, in order to more fully characterize visual field biases, primes were presented in eight positions around the target location. In both experiments, the primes were

presented briefly, and a visual mask was presented immediately after the primes in order to reduce top-down influences that are known to affect object identification (for discussion, see, e.g., Di Lollo, Enns, & Rensink, 2000; VanRullen & Koch, 2003). The goal was not to render prime stimuli "invisible" or "unconscious" but to limit the contribution of possible strategic factors that may operate when primes are fully visible.

Beyond testing the neurocognitive hypothesis that the left lateralization of tool knowledge may affect visual object processing, this set of experiments also permits an evaluation of an important theory about how tool concepts are represented. The embodied cognition hypothesis of tool recognition argues that the ability to recognize tools depends on simulation of motor-relevant information about how to manipulate those objects (Gallese & Lakoff, 2005; Kiefer & Pulvermüller, 2012; Pulvermüller, 2005; Simmons & Barsalou, 2003). A number of different types of evidence have been marshaled in support of that hypothesis; however, common to all of the data argued to support the embodied cognition hypothesis as it relates to tool recognition is the observation that motor-relevant information is automatically activated in the course of the visual processing of tools (see, e.g., Chao & Martin, 2000; for reviews, see Barsalou, 2008; Gallese & Lakoff, 2005; Martin, 2007; for a theoretical precedent, see Allport, 1985). We have argued (e.g., Mahon & Caramazza, 2008) that those data are ambiguous, in that they could indicate either (1) that visual recognition of a tool concept includes (representationally, or constitutively) motor-relevant information about how to manipulate objects (i.e., embodied hypothesis of tool recognition) or (2) that high-level visual representations subserving tool recognition have privileged connectivity with parietal structures that represent their associated manipulations and that the action-based information is retrieved subsequent to, or contingent on, visual recognition (for relevant findings, see Mahon et al., 2007).

Transcranial magnetic stimulation studies have sought to evaluate the involvement of motor representations during conceptual processing. For instance, Pulvermüller, Hauk, Nikulin, and Ilmoniemi (2005) found that stimulating somatotopic-specific sites (i.e., arm and leg sites) along motor cortex selectively affected lexical decisions for arm-related (e.g., *pick*) and leg-related (e.g., *kick*) words (respectively). Similarly, after stimulating motor cortex and measuring motor-evoked potentials (MEPs) in distal hand muscles, Oliveri, et al. (2004) found a selective increase in MEPs when participants passively read action verbs. Functional neuroimaging experiments also provide converging evidence that the motor system is involved, in a somatotopic-specific way, when observing (Buccino et al., 2001) or passively reading (Hauk, Johnsrude, & Pulvermüller, 2004) mouth-, arm-, and foot-related actions (for a review, see Barsalou, 2008;

Pulvermüller, 2005). Those studies show, decisively, that there is an association between motor system activation and the processing of action-related stimuli. However, it remains an open issue as to whether motor information forms a part (constitutively) of the conceptual representations of action words or whether spreading activation among conceptual and motor representations could explain the observed associations (e.g., Mahon & Caramazza, 2008).

The available neuropsychological data argue against strong forms of the embodied cognition hypothesis: Patient evidence indicates that damage to parietal regions can lead to impairments for using objects, while naming and categorizing the same objects can be spared (for reviews and discussions, see Chatterjee, 2010; Johnson-Frey, 2004; Mahon & Caramazza, 2005; Negri, Rumiati, et al., 2007; but see Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008). If those patient data are taken at face value, the hypothesis of privileged connectivity between the processes subserving high-level visual recognition of tools and knowledge of how to manipulate tools becomes more likely. Thus, if, in the priming experiments reported below, we were to observe a RVF bias for tools, those data would suggest that the bias is driven, at least in part, by interactions between brain regions that support visuomotor processing (dorsal stream) and brain regions that are known to be involved in visual object recognition and categorization (ventral stream).

Experiment 1

Method

Participants Seventeen University of Rochester undergraduate students (2 male) participated in the experiment in exchange for payment (age: 19–25 years, $M = 20.3$ years, $SD = 1.7$ years). Sixteen of the participants were strongly right-handed, as established with the Edinburgh Handedness Questionnaire (average handedness coefficient for right-handed participants = .94; average handedness coefficient for the left-handed participant = −.69). The participants all had normal or corrected-to normal vision and gave written informed consent in accordance with the University of Rochester Institutional Review Board.

Materials Sixty items (30 tools, 30 animals; see Supplemental Table 3) were used as stimuli for both primes and targets. The items were matched on lexical frequency (Celex; tools, $M = 20.2$, $SD = 37.2$; animals, $M = 22.8$, $SD = 30.6$; $t < 1$) and concept familiarity (MRC Psycholinguist Database; tools, $M = 519.3$, $SD = 62.4$; animals, $M = 519.8$, $SD = 33.9$; $t < 1$). Seventy percent additive noise was overlaid on the prime and target stimuli to facilitate the impact of the primes on the targets, as well as reduce their visibility (for a precedent for this

procedure, see Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008). Primes were always identical to target images; for the scrambled base-line, the identity prime was the image that was scrambled, in order to preserve all low-level visual information between the intact and scrambled conditions.

Testing apparatus The experiment was run on a desktop computer monitor (1,920 × 1,080 pixels; temporal resolu-tion = 60 Hz; viewing distance = 60 cm) using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) and a serial response box with millisecond precision (Psychology Software Tools). Target stimuli were presented centrally and subtended ~5° of visual angle; the prime and mask stimuli were the same size as the target stimuli, and the outside edges of the targets were ~0.28° from the inside edges of the prime and mask stimuli.

Design The design of Experiment 1 was a 2 (prime location: left, right) × 2 (category of target: animal, tool) × 2 (prime condition: identity, scrambled) within-subjects design. Each replication of the design was distributed over three blocks (80 trials/block, block duration ~6 min). Of the 80 trials within a block, half were animal and half tool targets, half identity primes and half scrambled primes, and half LVF primes and half RVF primes. Trial order within a block was random. One participant completed the design 9 times, and the remainder of participants completed the design 10 times (40,560 trials across all participants).

Procedure The experimenter first named each stimulus to the participant to ensure proper categorization in the experimental task; the experiment began immediately afterward. Figure 1

shows a schematic of the detailed trial structure. On each trial, a fixation cross appeared for a jittered amount of time (450, 550, 650, or 750 ms; 27, 33, 39, or 45 monitor refreshes); then the prime—a tool, an animal or a scrambled image of a tool or animal—was presented to the left or the right of the fixation cross for approximately 33 ms (2 monitor refreshes). When a prime (either intact or scrambled) was presented on either the left or the right, a scrambled image (within category) was presented in the opposite prime location. Bilateral stimulation was used to render it more difficult to determine on which side of the screen a prime had been presented. The result was that in the scrambled-prime condition, scrambled primes were pre-sented bilaterally, while in the identity-prime condition, an intact prime image (identical to the to-be-seen target) was presented on one side while a scrambled image was presented for the same duration on the opposite side. Immediately after the offset of the prime, a black-and-white high-contrast pattern mask was pre-sented in the same spatial location as the prime, and a different mask was presented simultaneously in the same location as the scrambled within-category image. The mask was on the screen for approximately 117 ms (7 monitor refreshes). Immediately upon the offset of the mask, the target image was presented in the center of the screen for 3 s or until a response was registered. Participants responded with their right index finger if the target was an animal and with their right middle finger if the target was a tool. They were instructed that they might see some flickering to the left and right of fixation but to focus on correctly identi-fying the target as quickly and accurately as possible.

After the completion of the main experiment, participants were debriefed that on some trials, primes had been briefly presented to the left or right of fixation before the target image. They then took part in a prime discrimination task. The trial structure and
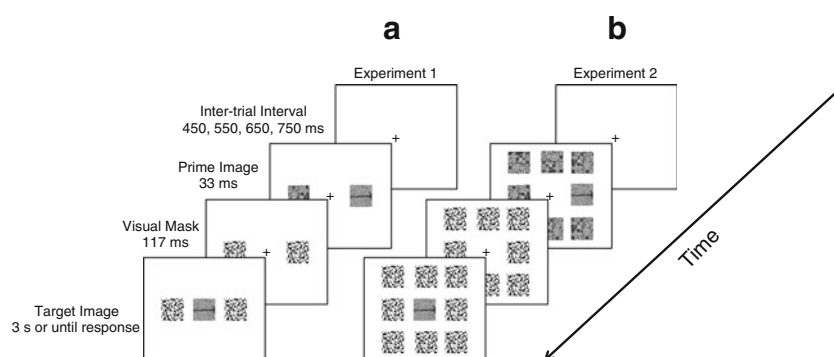

Fig. 1 Schematic of the trial structure in Experiment 1 and 2. **a** In Experiments 1 and 2, participants were instructed to categorize the target image as "tool" or "animal" with the index or middle finger of the right hand. Each trial began with a jittered fixation (450, 550, 650, or 750 ms). In Experiment 1, the prime was then presented to the left or right of fixation for 33 ms; in Experiment 2 (panel b), the prime was presented in one of eight locations arranged around central fixation. A scrambled image was presented at the same time as the prime in the other possible prime location(s). Visual masks were then presented

(duration = 117 ms) in the same location as the prime, as well as the locations of the scrambled stimuli. The offset of the mask was imme-diately followed by the target, which was on the screen for 3 s or until a response was given. In the follow-up prime discrimination task, the targets were replaced with question marks, and participants were told to discriminate the prime image when the question mark was pre-sented. The trial structure for the prime discrimination task was exactly the same as in the main experiment

procedure was the same, except that target images were replaced with a question mark and there was no scrambled-prime condition; participants completed 120 prime discrimination trials. Participants responded, when the question mark appeared, with their right index finger if the prime image was an animal and with their right middle finger if the prime image was a tool, indicating their "best guess" as to what had just been presented.

Results

Only correct response times (RTs) were analyzed (3.4 % of all trials were errors). Anticipations (RTs shorter than 200 ms) and outliers (greater than 2 standard deviations above and below the mean for each participant, calculated across all conditions) were removed (3.9 % of correct trials were excluded according to those criteria). RTs, priming effects, standard deviations, and error rates for each cell of the design are shown in Table 1.

A three-way ANOVA contrasted the factors prime location, target category, and prime condition. There was a main effect of prime condition, $F(1, 16) = 21.51$, $MSE = 142.11$, $p < .001$, indicating shorter RTs for identity primes than for scrambled primes. There was no main effect of target category, $F < 1$, and a trend toward a main effect of prime location, $F(1, 16) = 3.07$, $MSE = 39.93$, $p < .10$. The three-way ANOVA with the factors target category, prime location, and prime condition was marginally significant, $F(1, 16) = 4.16$, $MSE = 35.27$, $p = .058$.

Two separate two-way ANOVAs with the factors prime identity and prime location were carried out for tool and animal targets. For tools, there was a main effect of prime location, $F(1, 16) = 5.24$, $MSE = 31.18$, $p < .05$ (left-sided primes, 487 ms, $SD = 64$ ms; right-sided primes, 480 ms, $SD = 61$ ms), and prime identity, $F(1, 16) = 23.25$, $MSE = 69.6$, $p < .001$ (identity-prime trials, $M = 483$ ms, $SD = 62$ ms; scrambled-prime trials, $M = 493$ ms, $SD = 60$ ms). In addition, the interaction between prime location and prime identity was significant, $F(1, 16) = 5.75$, $MSE = 39.03$, $p < .05$. Planned contrasts (*t*-tests, two-tailed) collapsed the left-

and right-sided scrambled condition to form a single baseline condition for the derivation of priming effects. There were significant priming effects (identity RT < scrambled RT) for primes presented on the left, $t(16) = 3.74$, $p < .01$ (mean priming effect, 6.38 ms, $SD = 6.94$ ms), and on the right, $t(16) = 4.21$, $p < .01$ (mean priming effect, 13.12 ms, $SD = 11.33$ ms); consistent with the significant two-way interaction described above, right-sided tool primes led to greater priming effects than did left-sided tool primes, $t(16) = 3.21$, $p < .01$ (mean difference in priming effects, 6.73 ms, $SD = 8.66$ ms).

For animal targets, there was a main effect of prime condition, $F(1, 16) = 13.14$, $MSE = 109.73$, $p < .01$ (identity-prime trials, $M = 480$ ms, $SD = 53$ ms; scrambled-prime trials, $M = 490$ ms, $SD = 50$ ms), but no main effect of prime location (left-sided prime trials, $M = 481$ ms, $SD = 52$ ms; right-sided prime trials, $M = 480$ ms, $SD = 54$ ms), and no interaction between the two factors, $F < 1$. Thus, while identity animal primes elicited priming effects in general for animal targets, the magnitude of the priming effect was not modulated according to whether the prime was presented on the left or the right (see Fig. 2).

Prime discrimination data Overall, the primes were partially visible to participants, at least as their visibility was relevant to making a categorization decision over the prime pictures (average prime discrimination accuracy = 68 %; chance = 50 %; cutoff for significantly different than chance at $p = .05$ was 59 %; see Supplemental Table 1 for details). A 2×2 ANOVA contrasting prime location and prime category showed that neither the main effect of prime category, $F < 1$, nor that of prime location, $F(1, 16) = 1.78$, $MSE = .03$, $p > .20$, nor the interaction, $F < 1$, between the two factors was significant.

Discussion

Experiment 1 used lateralized primes together with a categorization task over tool and animal target pictures to test whether

Table 1 Mean response times (RT, in milliseconds), priming effects (in milliseconds), standard deviations (SD, in milliseconds), and error rates (%) by target category, prime location, and prime condition in Experiment 1

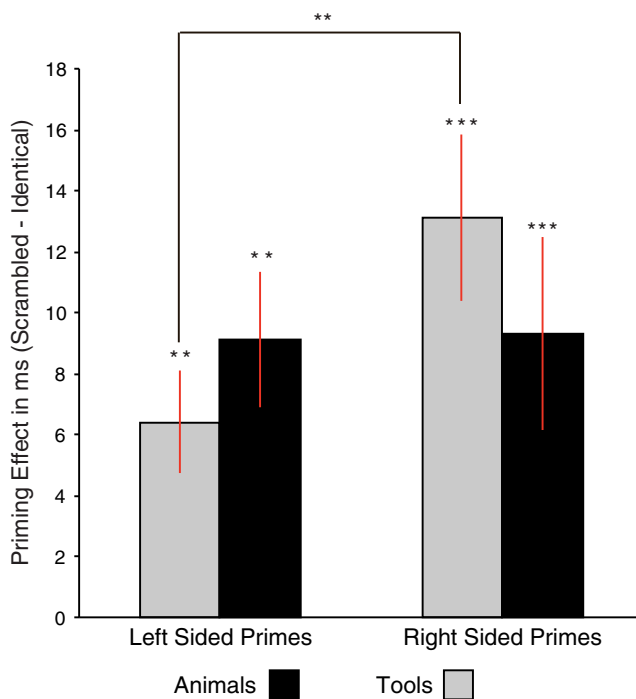|	Prime on the left						Prime on the right					
	Target category						Target category					
	Tool			Animal			Tool			Animal		
	RT	SD	%	RT	SD	%	RT	SD	%	RT	SD	%
Identity	487	64	.04	481	52	.03	480	61	.03	480	54	.04
Scrambled	493	60	.04	490	50	.03	493	60	.04	490	50	.03
Priming effect	6			9			13			10		

Fig. 2 Behavioral priming effects (scrambled − identity) for Experiment 1 displayed as a function of prime location and category. Error bars reflect standard errors of the means across participants. * $p < .05$; ** $p < .01$; *** $p < .001$

the known overrepresentation of tools in the left hemisphere affects visual object recognition. We observed that tool categorization was facilitated more when tool primes were presented on the right than when tool primes were presented on the left. In contrast, there was no modulation of categorization latencies for animal targets according to whether the primes were presented on the left or the right. The lack of modulation of animal categorization latencies by the location of the primes rules out a general RVF advantage in priming as being responsible for the pattern observed for tool targets.

In Experiment 2, we sought to replicate the principal finding of a RVF advantage for tool priming and to also more fully characterize visual field biases in tool processing by testing eight spatial positions around central fixation. There are some indications that the upper visual field may be overrepresented by processing in the ventral stream (Previc, 1990). Given that categorization of the target images is known to be subserved by ventral stream processes, it can be predicted that the RVF advantage for tool primes will be more pronounced for the upper visual field than for the lower visual field.

Experiment 2

Method

Participants Thirty-six University of Rochester undergraduate students (8 male) participated in the experiment in

exchange for payment (18–24 years old, $M = 19.8$ years, $SD = 1.7$ years). Thirty-five participants were strongly right-handed (average handedness coefficient for right-handed participants = .93; average handedness coefficient for the left-handed participant = −.81). All participants had normal or corrected-to-normal vision and gave written informed consent in accordance with the University of Rochester Institutional Review Board. One participant from Experiment 1 took part in Experiment 2, and 1 participant from Experiment 2 took part in control Experiment 2 (see below); all other participants did not overlap with any of the other experiments. The initial sample size for this experiment was 24 participants, at which point an interim analysis was conducted; however, in the context of addressing comments about those interim analyses, an additional 12 participants were added to Experiment 2 to increase statistical power, bringing the sample size to the current n of 36. This procedure, of analyzing data and then running additional participants, can increase the false positive rate (see Simmons, Nelson, & Simonsohn, 2011). We note that the addition of 12 participants did not qualitatively change the pattern of results and that the principal effects (described below) that are significant with 36 participants were significant with 24 participants.

Materials The same materials as those used in Experiment 1 were used in Experiment 2.

Design The experiment was a 2 (category of target: animal, tool) × 8 (prime location) × 2 (prime condition: identity, scrambled) within-subjects design. The full experimental design required 540 trials and was distributed over four blocks, with 135 trials per block. Each block contained 120 identity-prime trials and 15 scrambled-prime trials (baseline for priming effects). Of the 120 identity-prime trials, each animal stimulus and each tool stimulus was presented twice, each time in a different spatial location. The assignment of tool/animal stimuli to prime locations was chosen randomly for each block, with the constraint that all locations were equally represented across the four blocks. The 15 scrambled-prime trials switched between 8 tool and 7 animal scrambled trials (and vice versa) across the four blocks. On each scrambled baseline trial, eight different within-category scrambled primes were presented, one in each of the eight spatial positions. The 36 participants each replicated the four-block design 3 times (58,320 trials across all participants).

Procedure The central target and positions to the left and to the right of fixation subtended the same visual angle as in Experiment 1. The inside edge of prime and mask stimuli directly above and below the target was separated from the target by ~0.15° (outside edge of the target to inside edge of

the prime). The inside corners of primes and masks presented in upper and lower left and right diagonals were ~2° from the nearest corner of the central target. All other aspects of the procedure and trial structure were the same as in Experiment 1 (see Fig. 1b for details and a schematic of the trial structure).

After completion of the main experiment, participants were debriefed that on some trials, primes had been briefly presented across the visual field before the presentation of the target image. They then took part in a prime discrimination task. The trial structure and procedure was the same as in Experiment 2, except that target images were replaced with a question mark and there was no scrambled-prime condition; participants completed 480 prime discrimination trials (i.e., all stimuli were presented in each of the eight prime locations). The design of the 480 trials was identical to that in the preceding categorization experiment (for a total of four blocks of 120 trials). When the question mark appeared, participants responded with their right index finger if the prime image was an animal and with their right middle finger if the prime image was a tool, indicating their "best guess" as to what had just been presented.

Results

Trials on which the targets were miscategorized (7.7 % of all trials were removed) and outliers (following the same criteria as in Experiment 1; 4.5 % of correct trials) were excluded. Degrees of freedom were Greenhouse–Geisser corrected when Mauchly's test for violation of the assumption of sphericity was significant. RTs, priming effects, standard deviations, and percent correct trials are shown in Table 2.

A three-way ANOVA contrasted the factors prime condition, prime location, and target category. There was a main effect of prime condition, $F(1, 35) = 29.13$, $MSE = 1,425.87$, $p < .001$, indicating shorter RTs for identity primes than for scrambled primes. There was also a main effect of prime location, $F(4.68, 163.95) = 9.94$, $MSE = 129.56$, $p < .001$, but no main effect of target category, $F < 1$. Critically, the three-way interaction (target category, location of the prime, and prime condition) was significant, $F(7, 245) = 4.08$, $MSE = 77.17$, $p < .001$.

The two-way interaction (from the three-factor ANOVA described above) between target category and prime condition was not significant, $F < 1$, indicating that the magnitude of the priming effect did not vary for tools and animals. Thus, we calculated priming effects (scrambled-prime RTs− identity-prime RTs) separately for tools and animals and for each location and performed two separate one-way ANOVAs. Each ANOVA had eight levels (the eight locations). Critically, tool priming was modulated across the visual field, $F(7, 245) = 5.54$, $MSE = 148.76$, $p < .001$. In addition, and going beyond Experiment 1, animal priming was also modulated across the visual field, $F(4.58, 160.26) = 8.54$, $MSE = 273.62$, $p < .001$. See Fig. 3.

Planned contrasts (t-tests, two-tailed) were then carried out over priming effects (scrambled−identity primes). While there were significant priming effects (identity RT < scrambled RT) for tool primes presented on the left (collapsing across locations 6, 7, 8), $t(35) = 3.71$, $p < .001$, and on the right (collapsing across locations 2, 3, 4), $t(35) = 5.27$, $p < .001$, right-sided tool primes led to greater priming effects than did left-sided tool primes, $t(35) = 2.91$, $p < .01$. In contrast, while animal priming effects were significant on both the left, $t(35) = 3.83$, $p < .01$, and right, $t(35) = 2.03$, $p = .05$, priming for left-sided animal primes was greater than priming for right-sided animal primes, $t(35) = 4.49$, $p < .001$.

Four of the prime locations (directly above, below, to the left, and to the right) were located physically closer to the location of the subsequently presented targets, as compared with the other four prime locations (which occupied the

Table 2 Mean response times (RT, in milliseconds), priming effects (in milliseconds), standard deviations (SD, in milliseconds), and error rates (%) by location and stimulus category in Experiment 2

Prime Location	Response time						Standard deviation				Error rate			
	Identity		Scrambled		Priming effect		Identity		Scrambled		Identity		Scrambled	
	Tool	Animal	Tool	Animal	Tool	Animal	Tool	Animal	Tool	Animal	Tool	Animal	Tool	Animal
1	486	484	503	503	17	19	72	71	67	70	.03	.03	.04	.03
2	488	499	503	503	15	4	68	77	67	70	.04	.04	.04	.03
3	483	493	503	503	20	10	75	80	67	70	.04	.04	.04	.03
4	494	501	503	503	9	2	76	77	67	70	.03	.03	.04	.03
5	490	491	503	503	13	12	71	76	67	70	.04	.03	.04	.03
6	497	496	503	503	6	7	71	80	67	70	.04	.03	.04	.03
7	488	483	503	503	15	20	76	72	67	70	.03	.03	.04	.03
8	495	493	503	503	8	10	73	76	67	70	.04	.03	.04	.03

diagonals). Because it is known that physical proximity of primes to subsequently presented targets affects the magnitude of priming effects (Marzouki, Meeter, & Grainger, 2008), we tested for an effect of mere proximity of primes to targets. An ANOVA included the factors target–prime distance (close, far) and prime condition (identity, scrambled; collapsing across categories). There was a main effect of target–prime distance, $F(1, 35) = 40.74$, $MSE = 15.03$, $p < .001$, as well as a main effect of prime condition, $F(1, 35) = 29.13$, $MSE = 178.23$, $p < .001$. Importantly, analysis of the simple main effects showed priming effects for "close," $F(1, 35) = 43.58$,

$MSE = 107.50$, $p < .001$, and "far," $F(1, 23) = 13.05$, $MSE = 85.76$, $p < .01$, locations.

Prime discrimination data As in Experiment 1, participants were better than chance at prime discrimination (average prime discrimination accuracy = 72 %; chance = 50 %; cutoff for significantly different than chance at $p = .05$ was 55 %; see Supplemental Table 2 for details). A 2 × 8 ANOVA contrasting target category and prime location showed main effects of target category, $F(1, 35) = 11.51$, $MSE = 0.05$, $p < .01$, and prime location, $F(7, 245) = 6.40$,
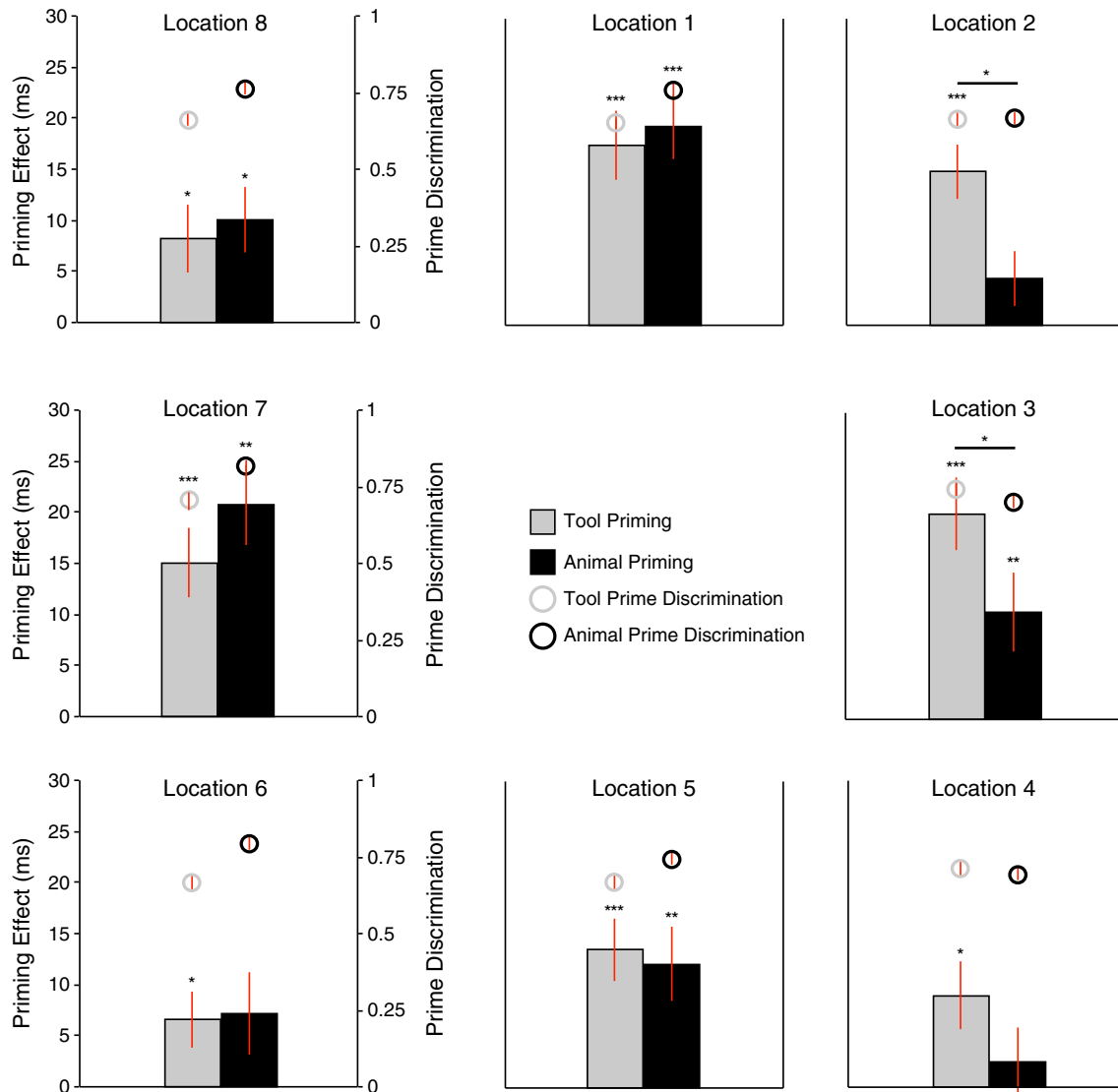

Fig. 3 Priming effects and prime discrimination in Experiment 2. Behavioral priming effects (scrambled − identity) and proportion correct prime discrimination are displayed by experimental condition. Error bars reflect standard errors of the means across participants. Planned contrasts (one-sample *t*-tests) depict significant priming effects for both tool and animal targets in locations 1 (directly above fixation), 3 (directly to the right of fixation), 5 (directly below fixation), and 7 (directly to the left of fixation) (all *p*s < .01). Tool priming effects

in the diagonals were all significant [prime location 2, upper right, $t(35) = 5.59$, $p < .001$; prime location 4, lower right, $t(35) = 2.69$, $p < .05$; prime location 8, upper left, $t(35) = 2.44$, $p < .02$; prime location 6, lower left, $t(35) = 2.39$, $p < .05$]. Analysis of animal priming effects in the diagonals found significant priming effects only for the upper left position, $t(35) = 3.15$, $p < .05$. All one-way *t*-tests reported as significant survived FDR correction ($q < .05$). Legend for alpha levels in figure: * $p < .05$; ** $p < .01$; *** $p < .001$

$MSE = 0.01$, $p < .001$, and a significant interaction, $F(5.21, 182.31) = 8.51$, $MSE = 0.13$, $p < .001$. These results indicate that including more prime locations in Experiment 2 resulted in prime visibility not being uniform across the visual field. We return to these data below.

Discussion

Experiment 2 replicated the principal pattern observed in Experiment 1, in which there was a RVF bias toward larger identity priming effects for tool targets. The RVF bias observed for tool targets was not observed for animal targets, which rules out a general RVF bias toward greater priming effects in general. Rather, if anything, animals showed the opposite bias as tools. While further work is necessary to pin down the properties of the possible asymmetry observed for animal stimuli in Experiment 2 (a bias toward stronger priming when primes are presented in the LVF), one might point toward the observation that differential neural responses to animals tend to be stronger in right-hemisphere regions (e.g., Anzellotti, Mahon, Schwarzbach, & Caramazza, 2011; Chao, Haxby, & Martin, 1999; Martin & Weisberg, 2003; Mormann et al., 2011; Noppeney et al., 2006).

Finally, and extending the results of Experiment 1, there were differences in prime visibility by location in the prime discrimination task. Inspection of the patterns present in Fig. 3 indicates that larger tool priming effects are associated with increased discrimination of the primes, across the eight possible prime locations. This positive relationship can

be quantified by correlating category biases in prime discrimination accuracy (animal prime discrimination proportion correct at each prime location minus tool prime proportion correct at each prime location) with the category bias in identity priming (animal priming effects at each prime location minus tool priming effects at each prime location) across the eight locations (linear $R^2 = .84$, $p < .01$; see Fig. 4). The fact that there is a relationship between prime discrimination accuracy and identity priming, in a category-specific manner across the visual field, reinforces and extends the principal finding: Visual object recognition for tools is differentially sensitive in RVF locations, both when accuracy is used (prime discrimination) and when RT is used (identity priming).

An objection that may be raised against the conclusion that identity priming for tool targets shows a RVF advantage is that participants may have adopted a strategy of initiating their categorization response upon the presentation of the prime, and not the target. This alternative account is *prima facie* reasonable in light of the fact that prime discrimination thresholds were above chance (albeit, slightly). Thus, it may be argued that the RVF advantage is not an effect due to priming per se but, rather, of categorizing a tool as a tool when presented on the right (with tool categorization decisions being initiated upon presentation of the prime). In order to address this objection, a control experiment was run in which tools were visibly presented either to the right or to the left of central fixation with no primes and participants ($n = 16$) were simply instructed to indicate whether a tool had been presented (go/no-go task). This type of

Fig. 4 Relationship between the difference in animal and tool prime discrimination and the difference in animal and tool identity priming (animal − tool). Those difference values are plotted by location of the primes in Experiment 2. Numbers below the data points refer to the location of the prime as schematized in Fig. 3. When the same analysis was carried out for each participant individually and the resulting r-values Fisher-transformed, the distribution of Fisher-transformed r-values across participants was significantly different from zero, $t(35) = 2.12$, $p < .05$
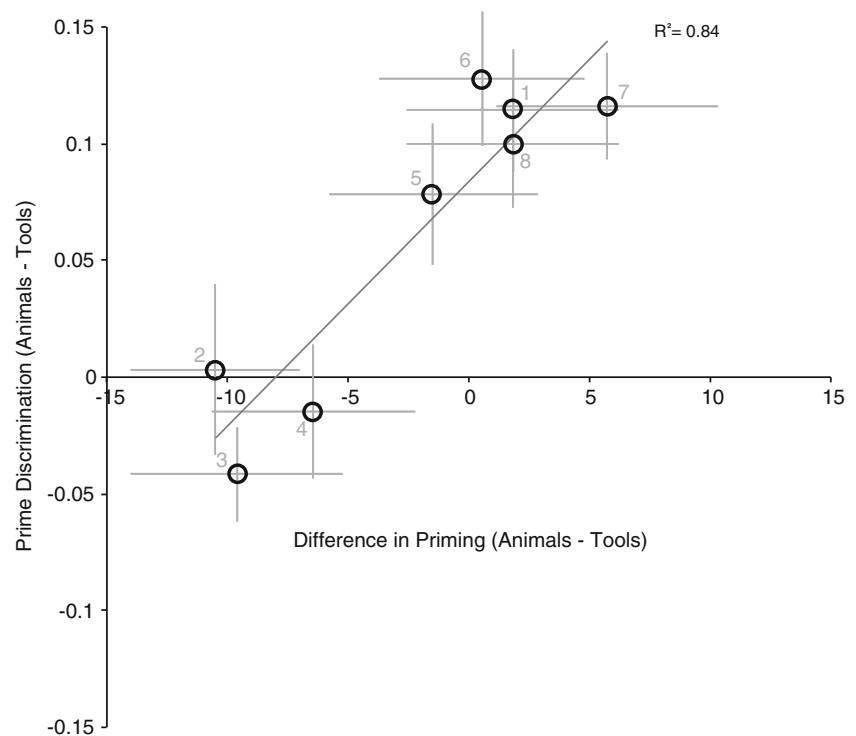
paradigm has previously been used (Thorpe, Fize, & Marlot, 1996) to demonstrate faster detection responses to faces than to other classes of stimuli. Thus, in order to have an internal control, we also included faces and places, as well as animals, as stimuli. Across blocks, participants were instructed as to which (of the four stimulus types) was the current "go stimulus"; they were to withhold a response when anything but the target category was presented and to push a button when the target stimulus was presented (see Supplemental Online Materials for all details). If the objection outlined above is valid, participants should be faster to detect the presence of a tool when it is presented in the RVF than when it is presented in the LVF. Contrary to that prediction, there were no differences for tool detection when tools were presented to the left or to the right of fixation, $t < 1$. However, and as first described by Thorpe and colleagues, detection of faces was faster than detection of tool, animal, and place stimuli, regardless of side of presentation (t-tests, two-tailed; all ps < .05; see Supplemental Fig. 1). Importantly, recognition of tools was not differentially modulated by the location of stimulus presentation (left-sided "go" tool trials, mean RT = 421 ms, SD = 43 ms; right-sided "go" tool trials, M = 426 ms, SD = 50 ms; $t < 1$). These data rule out an interpretation of the RVF bias toward larger identity priming for tool targets in terms of a *general speed advantage* for responding to tool images when presented in the RVF (see Table 3).

General discussion

Certain classes of stimuli are preferentially processed by the right or left visual field, according to whether they have a dominant representation in the left or right hemisphere. For instance, it is well known that the left hemisphere in most individuals is specialized for language and that printed words are processed faster and/or more efficiently in the RVF (Bub & Lewine, 1988; Chiarello, Nuding, & Pollock, 1988; Hunter & Brysbaert, 2008; Knecht et al., 2000). On the basis of neuropsychological and functional neuroimaging results, we outlined the hypothesis that the RVF would show an advantage for tools and that this advantage should

Table 3 Mean response times (RT, in milliseconds), standard deviations (SD, in milliseconds), and error rates (%) by location and stimulus category in Experiment 3

	Image on the left			Image on the right		
	RT	SD	%	RT	SD	%
Tools	421	43	.05	426	50	.06
Animals	435	53	.08	434	60	.07
Faces	398	46	.04	399	44	.02
Places	470	60	.13	472	51	.12

manifest in relatively larger priming effects for tool primes presented in the RVF. Our findings support this prediction and also show that the RVF advantage for tool targets is not a general RVF advantage for any type of stimulus (i.e., the RVF advantage was not observed for animal targets).

Given that prime discrimination thresholds were consistently above chance in Experiments 1 and 2, one issue that needs to be addressed is exactly how visible were the masked primes. In order to test whether participants are able to extract the identity of the primes from the degraded format in which they are presented, a second control experiment was run in which participants ($n = 19$) indicated whether a lateralized prime did or did not match a centrally presented word (for details, see Supplemental Online Materials). The same materials and procedures as those in Experiment 1 were used; the only difference was that the targets were capitalized words that shared the same identity as the primes or were within-category foils. Participants were at chance to decide whether the prime images and target words matched, regardless of whether the primes were presented in the RVF or the LVF (χ^2; across participants minimum p-value, .15; maximum p-value, .66). These data indicate that while participants were able to categorize the prime images at better-than-chance levels, in fact, little diagnostic information relevant to object identification was extractable from the degraded primes.

We reviewed findings in the introduction indicating that important aspects of conceptual and motor processes relevant to tool use are overrepresented in the left hemisphere (Boronat et al., 2005; Canessa et al., 2008; Chao & Martin, 2000; Handy et al., 2003; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Kellenbach et al., 2003; Kroliczak & Frey, 2009; Kroliczak et al., 2011; Mahon et al., 2007; Noppeney et al., 2006). We also discussed the embodied hypothesis of tool recognition, according to which simulation of the motor-relevant information about tool use in the dorsal stream is a necessary and intermediary step in the visual recognition of tools (e.g., Barsalou, 2008; Gallese & Lakoff, 2005; for a general discussion, see also Prinz, 1987). For instance, in a series of experiments, Helbig and colleagues (Helbig, Graf, & Kiefer, 2006; Helbig, Steinwender, Graf, & Kiefer, 2010) found that presentation of manipulable objects with congruent action-related properties improved accuracy to subsequently named objects. Participants were required to name a prime image and then a target image that immediately followed the prime image. Naming accuracy for trials with congruent target–prime relationships (e.g., *nutcracker–pliers*) was significantly better than naming accuracy for trials with incongruent target–prime relationships (e.g., *nutcracker–spoon*). Helbig et al. (2010) extended this effect when it was found that 2,000-ms movies depicting congruent action properties improved accuracy for a subsequently presented picture–word stimulus (participants had to indicate whether the

word matched the picture). On the basis of those findings, it was argued that motor-relevant information must be retrieved in order to recognize objects. However, we know on the basis of patient research that retrieval of motor information is not a necessary step in visual object recognition (e.g., Negri, Rumiati, et al., 2007; Ochipa, Rothi, & Heilman, 1989; Rothi, Ochipa, & Heilman, 1991).

The combination of findings that we have reported further refines an explanation of why the motor system is activated, and motor information automatically retrieved, when visual recognition tasks over manipulable objects are performed. On the assumption that categorization is subserved by ventral stream processes, the pattern of findings we have reported could be explained by assuming privileged connectivity between ventral stream regions and left-hemisphere parietal structures that represent object-associated manipulations. This conclusion would also suggest that priming effects such as those reported by Helbig, Keifer, and colleagues derive from connectivity between object recognition processes and motor-relevant information.

This interpretation resonates with the findings of Almeida et al. (2010; Almeida et al., 2008), who used a technique that blocked direct analysis of primes by ventral temporal structures but allowed direct access of the primes to dorsal structures (continuous flash suppression; Fang & He, 2005). Almeida et al. (2008) found that when primes were selectively presented to the dorsal stream, there was a priming effect for tool targets, and not for animal targets. What is common to the studies of Almeida and colleagues and our present study is the observation that signatures of dorsal stream processing can be observed on RTs for visual processing of manipulable objects.

It is important to consider an alternative explanation of our findings that does not appeal either to the embodied cognition hypothesis of tool recognition or to the idea that ventral–dorsal connectivity is the source of the RVF bias toward greater tool priming. Konen and Kastner (2008) found that parietal responses (using fMRI) to tool stimuli were invariant to image transformations. Invariance to image transformations is a property that one would expect of a system that is involved in visual recognition; or rather, and minimally, those data indicate that there are representations of objects in parietal cortex that are abstracted away from the visual input. Thus, it might be argued that object recognition occurs, at least in part, in parietal regions; since tool representations are known independently to be lateralized in the dorsal stream, that proposal could potentially explain the RVF advantage we have observed. While this interpretation of what might be occurring in the parietal cortex was not proposed by Konen and Kastner on the basis of their findings, it is important to consider whether such an account could explain our data. There are two arguments against this type of interpretation. First, lesions to parietal regions do not typically result in impairments for object recognition, while ventral stream lesions can impair object recognition. Second, in Experiment 2, the magnitude of the RVF advantage for tool priming was, if anything, larger in the upper visual field than in the lower visual field. On the assumption that upper visual field locations are more indicative of ventral stream processing, our data suggest that the more likely explanation of the observed variance in categorization latencies in this task is yoked to processes occurring in the ventral stream (for potentially relevant fMRI findings, see Koutstaal et al., 2001).

In summary, the observation of a RVF advantage for visual processing of tools in a categorization task suggests that while motor information may not be strictly necessary for visual object recognition, there may be important interactions between the motor and visual systems online during object recognition (Chatterjee, 2010; Kemmerer & Gonzalez Castillo, 2010; Mahon & Caramazza, 2008). This type of a model, in which there is dynamic information exchange between motor and visual representations, would provide an alternative framework for interpreting the oft reported finding that motor information is activated when manipulable objects are viewed. Importantly, it may be possible to directly evaluate this interpretation of the behavioral evidence we have reported by relating participant-by-participant variation in BOLD effects elicited by viewing tool stimuli in different cortical regions to participant-by-participant variation in the magnitude of the RVF advantage for tool primes.

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