

Running head: CONCEPTUAL KNOWLEDGE IN BLIND

1 **Different neural networks for conceptual retrieval in sighted and blind**

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Pages: 37

21 **# Words: Abstract (193); Introduction (642); Discussion (1469).**

22 **Acknowledgement:** This work was supported by a European Research Council
23 starting grant (MADVIS grant #337573) attributed to OC. OC is a research associate
24 at the Fond National de Recherche Scientifique de Belgique (FRS-FNRS). We wish to
25 extend our gratitude to the Michela Picchetti, Mattia Verri and Alberto Redolfi for the
26 technical support during fMRI acquisition. We are also extremely thankful to our blind
27 participants and the Unione Ciechi e Ipovedenti in Trento, Milano, Savona, Trieste,
28 and the Blind Institute of Milano. We also thank Yanchao Bi and Xiaoying Wang for
29 sharing brain maps from their previously published data.

30

31 **Author contributions:** R.B. and O.C. designed the research; R.B., S.F., A.N. and V.C.
32 performed the research; R.B. analyzed the data in interaction with O.C.; R.B. and O.C.
33 drafted the paper; all authors revised and edit the draft, and agreed on the final version
34 of the manuscript.

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1 **Abstract**

2 We investigated the experiential bases of knowledge by asking whether people that
3 perceive the world in a different way also show a different neurobiology of concepts.
4 We characterized the brain activity of early-blind and sighted individuals during a
5 conceptual retrieval task in which participants rated the perceptual similarity between
6 color and action concepts evoked by spoken words. Adaptation analysis showed that
7 word-pairs referring to perceptually similar colors (e.g., red-orange) or actions (e.g.,
8 run-jump) led to repetition-suppression in occipital visual regions in the sighted,
9 regions that are known to encode visual features of objects and events, independently
10 of their category. Early blind showed instead adaptation for similar concepts in
11 language-related regions, but not in occipital cortices. Further analysis contrasting the
12 two categories (color and action), independently of item similarity, activated category-
13 sensitive regions in the pMTG (for actions) and the precuneus (for color) in both sighted
14 and blind. These two regions, however, showed a different connectivity profile as a
15 function of visual deprivation, increasing task-dependent connectivity with reorganized
16 occipital regions in the early blind. Overall, our results show that visual deprivation
17 changes the neural bases of conceptual retrieval, which is partially grounded in
18 sensorimotor experience.

19

20 **Keywords:** Concepts; Color; Action; Blindness; Neuroplasticity; fMRI; Adaptation

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2 **Significance Statement:**

3 Do people with different sensory experience conceive the world differently? We
4 tested whether conceptual knowledge builds on sensory experience by looking at the
5 neurobiology of concepts in early blind individuals. Participants in fMRI heard pairs of
6 words referring to colors (e.g., green-blue) or actions (e.g., jump-run) and rated their
7 perceptual similarity. Perceptual similarity of colors and actions was represented in
8 occipital visual regions in the sighted, but in language-related regions in the blind.
9 Occipital regions in the blind, albeit not encoding perceptual similarity, were however
10 recruited during conceptual retrieval, working in concert with classic semantic hubs
11 such as the Precuneus and the lpMTG. Overall, visual deprivation changes the neural
12 bases of conceptual processing, which is partially grounded in sensorimotor
13 experience.

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1 **Introduction**

2 As we think, we navigate and retrieve conceptual knowledge, but the nature of
3 this knowledge is highly debated. One of the major sources of disagreement is whether
4 thinking is more similar to the analog replay of our experience (Barsalou, 1999;
5 Kosslyn, Ganis, & Thompson, 2001), or the symbolic computations of a Turing
6 machine (Fodor, 1975; Pylyshyn, 1984).

7 Congenital blindness offers an ideal model to test whether thinking is simulating
8 our own experience of the world (Barsalou, 2009; Lakoff & Johnson, 1999). If
9 conceptual processing is largely grounded into experience, blind people, who
10 experience the world in a different way, should also show a different neurobiology of
11 concepts, at least in part (Casasanto, 2011). Several studies, however, seem to
12 provide evidence against this idea (Bedny & Saxe, 2012). For instance, when sighted
13 and blind were asked to retrieve information about highly visual entities, knowledge
14 about small and manipulable objects (Peelen et al., 2013) activated the lateral
15 temporal-occipital complex; thinking about big non-manipulable objects activated the
16 parahippocampal place area (He et al., 2013); and processing action verbs (compared
17 to nouns) activated the left posterior middle temporal gyrus (Bedny et al. 2012) in both
18 groups. These results seem to suggest that blindness leaves the neurobiology of
19 conceptual retrieval largely unchanged, and that experience plays a minor role in
20 shaping mental representations (Bedny & Saxe, 2012; Uta Noppeney et al., 2003).

21 Alternatively, it is possible that previous studies relied on paradigms designed
22 to investigate categorical knowledge, a level of processing that is relatively resilient to
23 visual deprivation (Van Baelen, and Op de Beeck 2017). Indeed, categorical
24 boundaries (e.g., between objects, tools or animals) are drawn based on several
25 dimensions that exceed visual appearance (e.g., tokens from the same category do
26 not always look alike; Bracci and Op de Beeck 2016; Proklova, Kaiser, and Peelen

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1 2016), and depend on functional, emotional and linguistic constraints (Peelen &
2 Downing, 2017). Indeed, brain regions that show category specificity, seem to
3 represent different categories in a format that is at least partially independent from
4 visual appearance (Bracci & Op de Beeck, 2016), and thus more likely to be resilient
5 to visual deprivation (Bedny et al. 2012; van den Hurk, Van Baelen, and Op de Beeck
6 2017; Wang et al. 2015).

7 Differences between sighted and blind may be more likely to emerge when
8 participants process the perceptual similarity of retrieved concepts (Martin, Douglas,
9 Newsome, Man, & Barense, 2018), a process known to be encoded in more posterior
10 (visual) occipital regions in the sighted (Fernandino et al. 2015; Borghesani et al. 2016;
11 Mitchell et al. 2008). To test this hypothesis we asked sighted and early blind
12 participants to rate pairs of concepts based on their perceptual similarity and analyzed
13 the data using a repetition suppression framework (Barron, Garvert, and Behrens
14 2016; Wheatley et al. 2005; Grill-Spector, Henson, and Martin 2006). We reasoned
15 that this method will allow to tag selectively the representation of low-level perceptual
16 features during conceptual retrieval (Horner & Henson, 2011; Mohr, Linder, Linden,
17 Kaiser, & Sireteanu, 2009). We predicted that perceptually similar concepts (within a
18 given category) might elicit neural adaptation in the occipital cortex of sighted (who will
19 retrieve their visual similarity), but not blind people. On the other hand, a direct
20 comparison between categories (independently of visual/perceptual similarity) should
21 highlight category-specific responses in more anterior/multimodal areas of the brain,
22 with limited differences between sighted and blind. This should be especially true for
23 conceptual categories that can be perceptually experienced both by sighted and blind
24 individuals. Therefore, in our experiment, we choose stimuli exemplars coming from
25 actions and color categories. Including colors, that can be experienced through vision
26 only, allowed us to test whether their different epistemological status (concrete vs

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1 abstract), in sighted and blind, would influence their representation even in multimodal
2 areas of the brain that usually show resilience to visual deprivation (Striem-Amit,
3 Wang, Bi, & Caramazza, 2018).

4

5 **Materials and methods**

6 **Participants**

7 Thirty-six participants took part to this experiment: 18 early blinds (EB; 8F) and
8 18 sighted controls (SC; 8F). Participants were matched pairwise for gender, age, and
9 years of education (Table S1).

10 All the blind participants lost sight at birth or before 3 years of age and all of
11 them reported not having visual memories (Table S2). All participants were blindfolded
12 during the task. The ethical committee of the Besta Neurological Institute approved
13 this study (protocol fMRI_BP_001) and participants gave their informed consent before
14 participation.

15

16 **Stimuli**

17 We selected six Italian color words (*rosso/red*, *giallo/yellow*, *arancio/orange*,
18 *verde/green*, *azzurro/blue*, *viola/purple*), and six Italian action words (*pugno/punch*,
19 *graffio/scratch*, *schiaffo/slap*, *calcio/kick*, *salto/jump*, *corsa/run*). Words were all highly
20 familiar nouns and were matched across categories (color, action), by number of letters
21 (Color: mean= 5.83, sd= 0.98); Action: mean= 6, sd= 1.23), frequency (Zipf scale;
22 Color: mean= 4.02, sd= 0.61; Action: mean= 4.18, sd= 0.4), and orthographic
23 neighbors (Coltheart's N; Color: mean= 14, sd= 9.12; Action: mean= 15.33, sd= 12.42).

24 Auditory files were made using a voice synthesizer (talk to me), with a female
25 voice, and edited into separated audio files with the same auditory properties (44100
26 Hz, 32 bit, mono, 78 dB of intensity). The original duration of each audio file (range

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1 356 – 464 ms) was extended or compressed to 400 ms using the PSOLA (Pitch
2 Synchronous Overlap and Add) algorithm and the sound-editing software Praat
3 (Boersma & Weenink, 2018). All the resulting audio files were highly intelligible.

4

5 **Experimental Design**

6 We designed a fast event-related fMRI paradigm during which participants
7 listened to pairs of color and action words. In each trial the two words were played one
8 after the other with a stimulus onset asynchrony (SOA) of 2000 ms.

9 The inter-trial interval ranged between 4000 and 16000 ms. Participants were
10 asked to judge the similarity of the two colors or the two actions from 1 to 5 (1: very
11 different, 5: very similar). Responses were collected via an ergonomic hand-shaped
12 response box with five keys (Resonance Technology Inc.). All participants used their
13 right hand to provide responses (thumb = very different, pinky = very similar).
14 Participants were told that they had about 4 seconds to provide a response after the
15 onset of the second word of the pair and they were encouraged to use all the scale (1
16 to 5). Furthermore, the instruction was to judge the similarity of colors and actions
17 based on their perceptual properties (avoiding reference to emotion, valence, or other
18 non perceptual characteristics). Blind participants were told to judge color pairs on the
19 basis of their knowledge about the perceptual similarity between colors.

20 Color and action words were presented in all possible within-category
21 combinations (15 color pairs, 15 action pairs). Each pair was presented twice in each
22 run, in the two possible orders (e.g., red-yellow, yellow-red). Thus, there were 60 trials
23 in each run and the experiment consisted in 5 runs of 7 minutes. Stimuli were
24 pseudorandomized using optseq2 to optimize the sequence of presentation of the
25 different conditions. Three different optimized lists of trials were used across runs. List
26 order was counterbalanced across subjects.

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1 One early blind was excluded from the analyses because the subject answered
2 to less than 70% of the trials throughout the experiment due to sleepiness. One run of
3 one sighted subject was excluded from the analysis because of a technical error during
4 the acquisition, and two other runs (one in a sighted subject, one in a blind subject)
5 were excluded since the subject answered to less than 70% of the trials in that specific
6 run.

7

8 **Conceptual similarity ratings**

9 In order to perform the adaptation analysis, we divided the trials in similar pairs
10 (e.g. red - orange) and different pairs (e.g. red - blue). We did so based on the
11 participants' subjective ratings. For each participant we took the average rating for
12 each of the 15 word-pairs in the action and color categories. Then we automatically
13 divided the 15 pairs in 5 intervals (4 quantiles) of nearly equal size. This subdivision
14 was performed using the function *quantile*, in R (R Core Team, 2013), that divides a
15 probability distribution into contiguous intervals of equal probabilities (i.e., 20%). The
16 pairs in the first two intervals were the different pairs (low ratings of similarity), the pairs
17 in the 3rd interval were the medium pairs, and the pairs in the 4th and 5th intervals were
18 the similar pairs (See fig 2B). However, in some cases, ratings distributions were
19 slightly unbalanced, due to the tendency of some subjects to find more “very different”
20 pairs than “very similar” pairs. In these cases (8 subjects for action ratings [3 EB]; 4
21 subjects for Color Ratings [1 EB]), the automatic split in 5 equal intervals was not
22 possible. Thus, we set the boundary between the 2nd and 3rd interval at the ratings
23 average (for that given subject), and set to the minimum (1 or 2, depending on the
24 cases) the number of items in the 3rd interval (not analyzed), in order to balance as
25 much as possible the number of pairs in the Different and Similar groups. This
26 procedure made so that in these special cases (as well as in all the others), the rating

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1 values of different pairs were always below the mean, and the values of similar pairs
2 was always above the mean. Fig. S4, S5, S6, S7, in the supplementary information,
3 show subject-specific rating distributions.

4

5 **MRI data acquisition**

6 Brain images were acquired at the Neurological Institute Carlo Besta in Milano
7 on a 3-Tesla scanner with a 32-channel head coil (Achieva TX; Philips Healthcare,
8 Best, the Netherlands) and gradient echo planar imaging (EPI) sequences.

9 In the event-related experiment, we acquired 35 slices (voxel size 3 X 3 X 3.5)
10 with no gap. The data in-plane matrix size were 64 X 64, field of view (FOV) 220mm X
11 220mm, time to repetition (TR)= 2 s, flip angle 90 degrees and time to echo (TE)= 30
12 ms. In all, 1210 whole-brain images were collected during the experimental sequence.
13 The first 4 images of each run were excluded from the analysis for steady-state
14 magnetization. Each participant performed 5 runs, with 242 volumes per run.

15 Anatomical data was acquired using a T1-weighted 3D-TFE sequence with the
16 following parameters: 1 X 1 X 1 mm voxel size, 240 X 256 matrix size, 2.300 ms TR,
17 2.91 ms ET, 900 ms TI, 256 FoV, 160 slices.

18

19 **MRI data analysis**

20 We analyzed the fMRI data using SPM12 ([www.](http://www.fil.ion.ucl.ac.uk/spm/software/spm12/)
21 fil.ion.ucl.ac.uk/spm/software/spm12/) and Matlab R2014b (The MathWorks, Inc.).

22 **Preprocessing.** Preprocessing included slice timing correction of the functional time
23 series (Sladky et al., 2011), realignment of functional time series, coregistration of
24 functional and anatomical data, spatial normalization to an echoplanar imaging
25 template conforming to the Montreal Neurological Institute (MNI) space, and spatial
26 smoothing [Gaussian kernel, 6 mm full-width at half-maximum (FWHM)]. Serial

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1 autocorrelation, assuming a first-order autoregressive model, was estimated using the
2 pooled active voxels with a restricted maximum likelihood procedure, and the
3 estimates were used to whiten the data and design matrices.

4 **Data analysis.** Following preprocessing steps, the analysis of fMRI data,
5 based on a mixed-effects model, was conducted in two serial steps accounting,
6 respectively, for fixed and random effects. In all the analysis the regressors for the
7 conditions of interest consisted of an event-related boxcar function convolved with the
8 canonical hemodynamic response function according to a variable epoch model
9 (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008). Movement parameters derived
10 from realignment of the functional volumes (translations in x, y, and z directions and
11 rotations around x, y, and z axes), and a constant vector, were also included as
12 covariates of no interest. We used a high-pass filter with a discrete cosine basis
13 function and a cutoff period of 128 s to remove artifactual low-frequency trends.

14 **Adaptation analysis:** For each subject, the general linear model included 6
15 regressors corresponding to the 3 levels of similarity (different, medium, similar) in
16 each condition (color, action). Color and Action pairs in the medium condition were
17 modeled as regressors of no interest.

18 At the first level of analysis, linear contrasts tested for Repetition Suppression
19 [Different > Similar] collapsing across categories (Action, Color). The same contrasts
20 were then repeated within each category [Color Different > Color Similar; Action
21 Different > Action Similar]. Finally, we tested for the Similarity by Category interactions,
22 testing whether the adaptation was stronger in one category compared to the other
23 (e.g., [Color Different > Color Similar] > [Action Different > Action Similar]).

24 These linear contrasts generated statistical parametric maps [SPM(T)]. The
25 resulting contrast images were then further spatially smoothed (Gaussian kernel 5mm
26 FWHM) and entered in a second-level analysis (RFX), corresponding to a random-

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1 effects model, accounting for inter-subject variance. One-sample t-tests were run on
2 each group separately. Two-sample t-tests were then performed to compare these
3 effects between groups (Blind vs Sighted).

4 **Univariate analysis:** For each subject, changes in regional brain responses
5 were estimated through a general linear model including 2 regressors corresponding
6 to the two categories Action and Color. The onset of each event was set at the
7 beginning of the first word of the pair, the offset was determined by the subject
8 response, thus included reaction time (Grinband et al., 2008). Linear contrasts tested
9 for action-specific [Action > Color] and color-specific [Color > Action] BOLD activity.

10 These linear contrasts generated statistical parametric maps [SPM(T)]. The
11 resulting contrast images were then further spatially smoothed (Gaussian kernel 5mm
12 FWHM) and entered in a second-level analysis, corresponding to a random-effects
13 model, accounting for inter-subject variance. One-sample t-tests were run on each
14 group separately. Two-sample t-tests were then performed to compare these effects
15 between groups (Blind vs Sighted) and to perform conjunction analyses to observe if
16 the two groups presented similar activated networks for the two contrasts of interests.

17 **Connectivity analysis:** Psychophysiological interaction (PPI) analyses were
18 computed to identify brain regions showing a significant change in the functional
19 connectivity with seed regions (the right precuneus, the left pMTG and the rIPS) that
20 showed a significant activation ($p < .001$, uncorrected) in the [(EB Conj. SC) X (Color >
21 Action)] contrast, the [(EB Conj. SC) X (Action > Color)] contrast, and the [(SC > EB)
22 X (Action > Color)] contrast respectively. In each individual, time series of activity
23 (principal eigenvariate) were extracted from a 8 mm sphere centered on the nearest
24 local maxima to the identified peaks in the second-level analysis (Note that centering
25 the sphere on the peak itself does not change the ROI Analysis results, see
26 Supplementary Information). New linear models were generated at the individual level,

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1 using three regressors. One regressor represented the psychological condition of
2 interest (action or color trial). The second regressor was the physiological activity
3 extracted in the reference area. The third regressor represented the interaction of
4 interest between the first (psychological) and the second (physiological) regressor. The
5 design matrix also included movement parameters and a constant vector as regressors
6 of no interest. A significant PPI indicated a change in the regression coefficients
7 between any reported brain area and the seed region, related to the experimental
8 conditions (Color>Action or Action>Color). Next, the individual summary statistic
9 images obtained at the first-level (fixed-effects) analysis were spatially smoothed (5
10 mm FWHM Gaussian kernel) and entered in a second-level (random-effects) analysis
11 using a two-sample t test contrasting the two groups.

12 **ROI definition.** Occipital ROI for the PPI analyses were defined as following.
13 Two peak-coordinates were taken from previous studies (Bedny et al. 2011; Kanjlia et
14 al. 2016) showing the involvement of EB occipital areas in high-level functions such as
15 language (left MOG [-36, -90, -1]) and mathematics (right MOG [33, -82, 9]). These
16 areas also showed increased long range connectivity (in early blind) with frontal and
17 parietal areas during rest (Bedny et al. 2011; Kanjlia et al. 2016; Liu et al. 2007;
18 Collignon et al. 2013).

19 The V4 and V5 ROI were drawn from the literature, considering both perceptual
20 localizers, as well as evidence from semantic/conceptual task. We selected 3 peak
21 coordinates for area V5. The first [-47, -78, -2] from a highly-cited study contrasting the
22 perception of visual motion vs static images (Dumoulin et al., 2000). The second [-44,
23 -74, 2] from a study (Saygin, McCullough, Alac, & Emmorey, 2010) showing V5
24 sensitivity to motion sentences (e.g., “The wild horse crossed the barren field”). The
25 third from a research on the on-line meta-analysis tool Neurosynth
26 (<http://neurosynth.org/>) for the topic “action”. In Neurosynth, the area in the occipital

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1 cortex with the highest action-related activation was indeed V5 (peak coordinates: -50,
2 -72, 2). To avoid ROI proliferation, we averaged these 3 peak-coordinates in order to
3 obtain a single peak (average peak: -47, -75, 1).

4 As for V4, we selected the color-sensitive occipital ROI considering perceptual
5 localizers, as well as evidence of color-specific activity from semantic/conceptual task.
6 Fernandino et al. (Fernandino et al., 2015) reported a color sensitive area in the left
7 posterior collateral sulcus (CoIS; at the intersection between the Lingual and the
8 Fusyform gyrus; MNI peak coordinates: -16, -71, -12) associated with color-related
9 words. This peak is close to the posterior-V4 localization done by Beauchamps and
10 colleagues (peak coordinates: -22, -82, -16) in a MRI version of the Farnsworth–
11 Munsell 100-Hue Test (Beauchamp, Haxby, Jennings, & DeYoe, 1999). A search in
12 neurosynth with the keyword “color” also highlighted a left posterior color-sensitive
13 region along the CoIS with peak coordinates [-24, -90, -10]. We averaged these 3
14 peaks to find the center of our region of interest (average peak: -21, -81, -13).

15 The posterior lateral-temporal cortex ROI (PLTC) was taken from 3 studies
16 showing semantic repetition suppression in that area. Bedny and colleagues (Bedny,
17 McGill, and Thompson-Schill 2008) observed increased neural adaptation in PLTC
18 (peak coordinates: 57, -36, 21) for repeated words (fan - fan), when the words were
19 presented in a similar context (summer – fan; ceiling - fan), compared to when different
20 context triggered different meanings (e.g., admirer – fan; ceiling – fan). This result
21 conceptually replicated previous studies (Kotz, Cappa, Cramon, & Friederici, 2002;
22 Wible et al., 2006) showing semantic adaptation in the bilateral PLTC for related (e.g.,
23 dog - cat) vs unrelated (e.g., dog - apple) word pairs (peak coordinates: -42, -27, 9 and
24 -51, -22, 8). These 3 peaks were averaged to find the center of our region of interest
25 in both hemispheres (average peak: ± 50 , -28, 13).

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1 **Statistical analysis.**

2 At the whole brain level, statistical inference was made at a corrected cluster
3 level of $P < 0.05$ FWE (with a standard voxel-level threshold of $P < 0.001$ uncorrected)
4 and a minimum cluster-size of 50 voxels. ROI analysis based on Small Volume
5 Correction were thresholded at $p < 0.05$ FEW at the voxel level.

6 All ROI analyses were performed using Small Volume Correction using
7 spheres with a 10mm radius centered around the ROI peak coordinates (see previous
8 session). Within the ROI, results were considered significant at a threshold of $p < 0.05$,
9 FEW-corrected. Here, and throughout the paper, brain coordinates are reported in MNI
10 space.

11 Behavioral data, analysis code and t-maps from the main contrasts will be
12 made available on-line (<https://www.biorxiv.org/content/early/2018/08/23/384552>).
13 Row fMRI images will be made available upon request, following agreements with our
14 ethical board committee.

15

16 **Results**

17 **Within-category similarity is encoded in occipital areas in the sighted but not in**
18 **the blind.** The rationale behind adaptation analyses was that the direct contrast
19 between pairs with high versus low perceptual differences will display neural
20 adaptation (Barron et al., 2016; Grill-Spector, Henson, & Martin, 2006; Wheatley,
21 Weisberg, Beauchamp, & Martin, 2005) therefore probing regions that are specifically
22 sensitive to the *perceptual distance* between concepts.

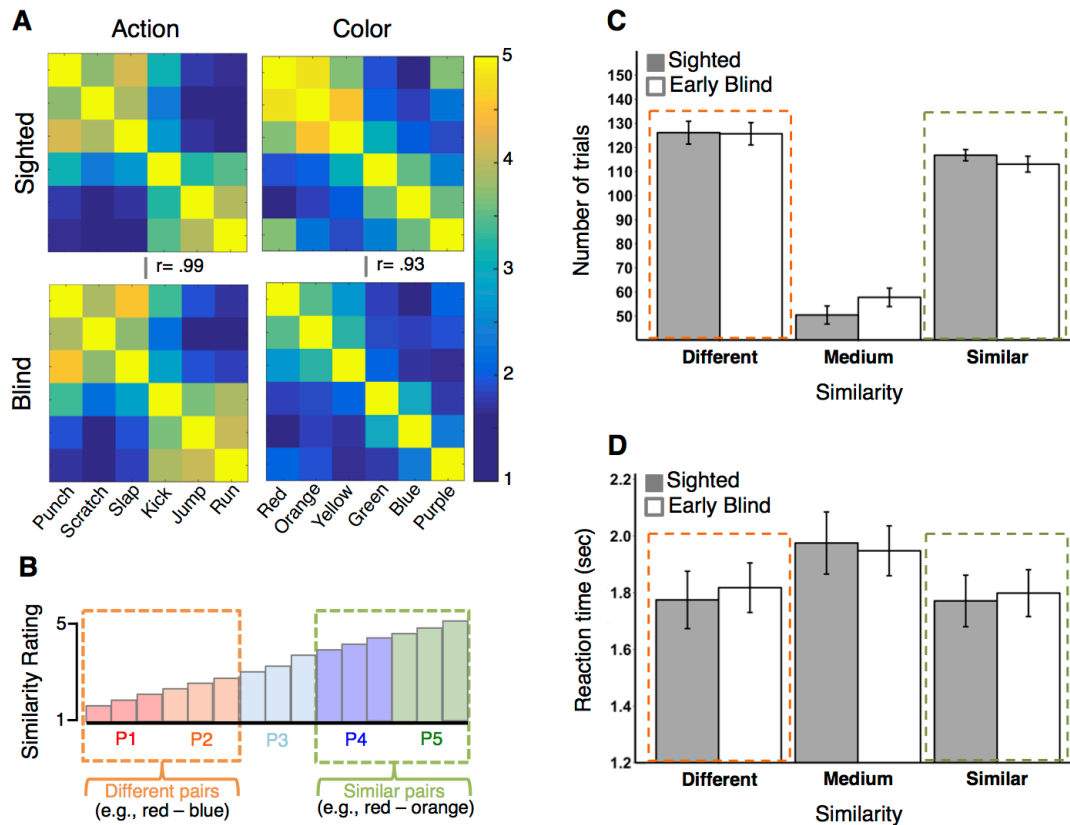
23 *Behavioral analysis:* Similarity ratings were highly correlated between sighted and
24 blind, both for action ($r = .99$) and color concepts ($r = .93$; Fig. 1A). In order to perform
25 the adaptation analysis we divided the trials in similar pairs (e.g. red - orange) and
26 different pairs (e.g. red - blue), based on each participant' subjective ratings. Rating

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1 distributions for each subject and category (color, action) were divided in 5 intervals
2 with a similar number of items (see Method session for details). Stimulus-pairs in the
3 first two intervals were labeled as different (low similarity ratings), the 3rd interval
4 contained medium pairs, and the 4th-5th intervals similar pairs (high similarity ratings;
5 Fig 1B). Overall, the average number of “different” trials was slightly larger than the
6 “similar” ones (126 vs 115; $F(1,33)=8.41$, $p=0.007$, $\eta^2=0.20$; Fig. 1C). However, there
7 was no similarity by group interaction ($F(1,33)=0.18$, $p=0.67$, $\eta^2=0.004$), indicating
8 that this unbalance (that reflected personal judgments of similarity) was the same
9 across SC and EB (fig. 1C). An analysis of reaction times showed that Medium pairs
10 (not analyzed in fMRI) had on average longer latencies than Similar and Different ones
11 (Main Effect of Similarity: $F(2,66)=21.07$, $p<0.001$, $\eta^2=0.38$). This was expected since
12 pairs that are neither similar nor different would require longer and more difficult
13 judgments. Crucially, there was no difference in reaction times between different
14 (Mean=1.80 sec, SD=0.39) and similar pairs (Mean=1.79 sec, SD=0.37; $F(1,33)=0.09$,
15 $p=0.76$, $\eta^2=0.003$), and no interaction between Similarity and Group ($F(1,33)=0.04$,
16 $p=0.84$, $\eta^2=0.001$; Fig 1D).

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2 **Figure 1. Adaptation, behavioral analysis.** (A) Similarity judgments were highly correlated
 3 across groups both for actions and color; (B) Conceptual schema of the division of word pairs
 4 in “different” and “similar” based on subjective similarity ratings; (C) Barplot depicting the
 5 average number of items in the “different”, “medium” and “similar” categories. The number of
 6 items in the “different” and “similar” categories is very similar across groups (number of trials \pm
 7 SEM); (D) Barplot depicting the average reaction time in the “different”, “medium”, and “similar”
 8 categories. The average RTs of the “different” and “similar” categories is very similar across
 9 groups (seconds \pm SEM).

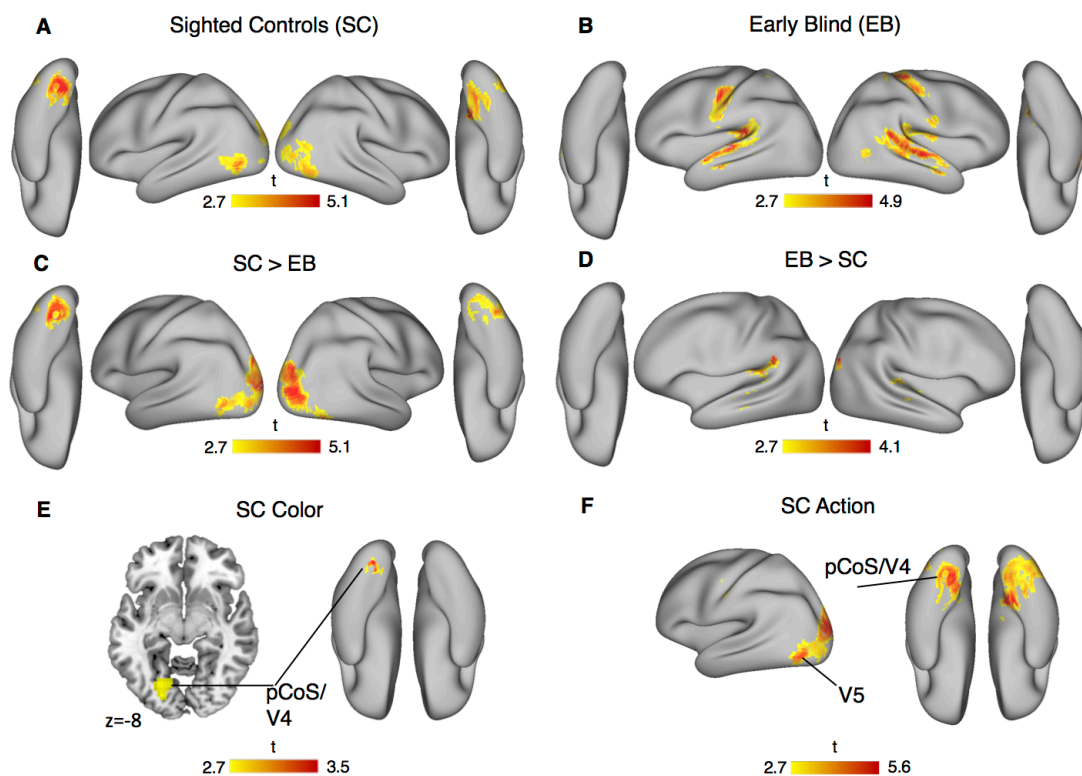
10

11 *fMRI analysis:* to find brain areas that showed adaptation based on conceptual
 12 similarity, we looked at the contrast Different Pairs > Similar Pairs, with Medium pairs
 13 as a regressor of no interest. Action and color pairs were considered together since,
 14 at the whole brain level, we did not find a significant higher-order interaction between
 15 Similarity (different, similar) and Category (see the method section for analysis details).
 16 In the sighted, similar concepts led to repetition suppression in several occipital areas
 17 (See Fig. 2A), with a significant cluster in and around the left lingual gyrus (peak
 18 coordinates: -24, -70, -7). In the blind, instead, adaptation emerged in language-related
 19 areas with significant clusters along the middle and superior temporal gyrus, bilaterally

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1 (Peak coordinates RH: 57, -28, 8; LH: -60, -10, -7) and in the right precentral gyrus
2 (Peak coordinates: 27, -25, 56; Fig. 2B). Importantly, no adaptation in posterior
3 occipital areas was observed in the blind.

4 A comparison between groups showed greater adaptation in occipital cortices
5 for sighted compared to blind (Fig. 2C), with peaks in the left superior occipital gyrus
6 (-24, -91, 26), the left lingual gyrus (-24, -70, -7) and the right middle occipital gyrus
7 (27, -85, 11). The contrast Blind > Sighted showed increased adaptation in posterior
8 lateral temporal cortices (PLTC) bilaterally (Fig. 2D). Planned ROI analysis in PLTC, a
9 region that consistently show repetition suppression for semantic similarity (Bedny,
10 McGill, and Thompson-Schill 2008; Wible et al. 2006; Kotz et al. 2002), revealed a
11 significantly greater adaptation for similar concepts in blind more than sighted
12 (Conceptual Similarity by Group interaction; lPLTC= -45 -31 20, $t(33)=3.23$, $P=0.035$;
13 rPLTC= 45 -28 11, $t(33)=3.41$, $P=0.024$).



14

15 **Figure 2. Adaptation, fMRI results.** Regional BOLD responses are rendered over Conte-
16 69 average midthickness surfaces. (A) Suprathreshold clusters showing neural adaptation for

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1 similar word pairs in the occipital cortices of sighted participants; (B) Suprathreshold clusters
2 showing neural adaptation for similar word pairs in the temporal and somatosensory-motor
3 cortices of early blind participants; (C) Suprathreshold clusters showing neural adaptation for
4 similar word pairs in sighted compared to blind, and (D) blind compared to sighted; (E)
5 Suprathreshold cluster showing neural adaptation for similar color-word pairs in the sighted,
6 with regional activity precisely localized in the left PCoS/V4 (see Fernandino et al. 2015 for a
7 very similar result with a multivariate design); (F) Suprathreshold clusters showing neural
8 adaptation for similar action-word pairs in the sighted, with regional activity spread in different
9 occipital areas including the left PCoS/V4 and the left V5. Cluster threshold at $P < 0.005$
10 uncorrected, for illustration only.
11

12 Finally, we performed planned ROI analysis in the color-sensitive region at the
13 posterior banks of the collateral sulcus (PCoS) corresponding to the V4-complex
14 (Beauchamp et al., 1999; Fernandino et al., 2015) and the motion sensitive region V5
15 (Dumoulin et al., 2000). In area PCoS-V4 we found greater adaptation both for color
16 and action in sighted compared to blind (Conceptual Similarity by Group interaction;
17 peak= -24 -73 -10, $t(33)=4.26$, $P= 0.004$; Fig 2 E-F). In contrast, the analysis in V5
18 showed that repetition suppression was specific for action concepts in the sighted and
19 no adaptation was observed in the blind (Conceptual Similarity by Group by Category
20 interaction; Peak: -51 -76 8, $t(33)=3.29$, $P= 0.037$; Fig 2F).

21

22 **Brain regions active in sighted and blind when contrasting action and color**
23 **concepts.** Subsequently we ran classic univariate analysis, comparing items across
24 categories independently of their similarity, to find category-specific activations across
25 sighted and blind. In these analyses, the two words in each pair were considered as a
26 single trial.

27 *Behavioral analysis:* Reaction times analysis using a mixed ANOVA, with Category
28 (action, color) as within-subject factor and Group (sighted, blind) as between-subjects
29 factor, showed no difference between categories ($F(1,33)=2.37$, $p>0.05$, $\eta^2= 0.07$),
30 between groups ($F(1,33)=0.074$, $p>0.05$, $\eta^2=0.002$) and no Category by Group
31 interaction ($F(1,33)=0.69$, $p>0.05$, $\eta^2=0.02$).

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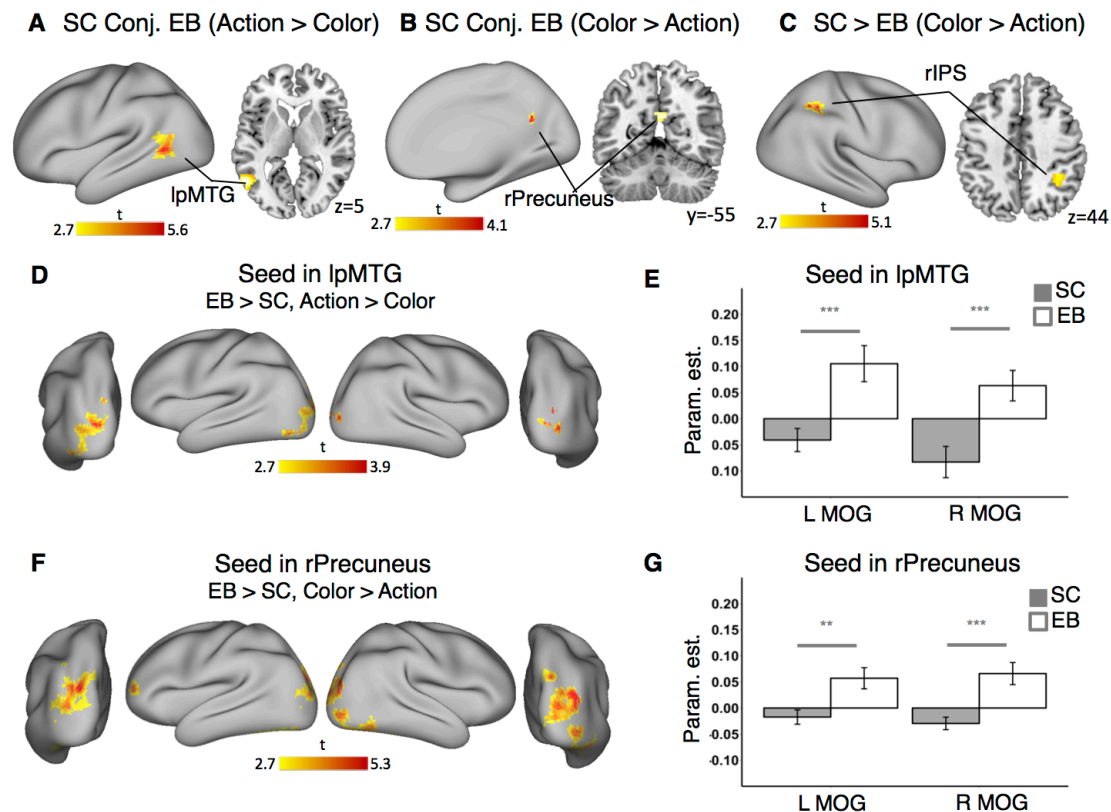
1 *fMRI analysis*: The contrast Action > Color did not reveal any significant difference
2 between groups, suggesting a comparable categorical representation of action
3 concepts, across sighted and blind (see fig. S2 for details). Indeed, a conjunction
4 analysis between groups showed a common significant activation in the left posterior
5 middle temporal gyrus (lpMTG; Peak= -54, -61, 5; Fig 3A).

6 On the other hand, a conjunction analysis between groups for Color > Action
7 did not reveal any common activation between sighted and blind after correction for
8 multiple comparisons at the whole brain level. However, displaying the conjunction
9 results at a more lenient threshold ($p < .001$ uncorrected; Fig 3C), we could notice a
10 unique common activity for color concepts in the right precuneus (peak= 6, -55, 26).
11 Accordingly, analysis within groups showed a significant precuneus activity in the blind
12 (peak= 6, -52, 20, $p = .04$) and a marginally significant activity in the sighted (peak= 0,
13 -61, 29, $p = .06$), with no significant difference between groups (Table S1; Fig. S1).

14 Further analysis for the contrast Color > Action revealed a cluster in the right
15 parietal cortex, in and around the right intraparietal sulcus (rIPS), showing higher
16 activity for color concepts in sighted compared to blind (peak= 33, -43, 35; Fig. 3B).

17 Altogether these results show similar patterns of activity during conceptual
18 processing in sighted and blind, when categorical preferences are investigated
19 (independently of perceptual similarity). As in previous results (Bedny et al., 2012; Uta
20 Noppeney et al., 2003; van den Hurk et al., 2017) such common activities are found
21 outside the posterior occipital cortex, in areas that are considered to be highly
22 polymodal such as the precuneus and the lpMTG (Binder, Desai, Graves, & Conant,
23 2009). Interestingly, even at this level of comparison we could find an effect of visual
24 deprivation, concerning color knowledge, that seem to involve the right IPS more in
25 sighted than blind.

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1

2 **Figure 3. Contrasts between categories and psychophysiological interactions.** Regional
3 BOLD responses are rendered over Conte-69 average midthickness surfaces. (A)
4 Suprathreshold cluster ($P < 0.05$ FEW corrected) showing common activity in the lpMTG for the
5 contrast Action > Color in both sighted and early blind (conj., conjunction analysis); (B)
6 Suprathreshold cluster ($P < 0.001$ uncorrected; for illustrative purposes only) showing common
7 activity in the precuneus for the contrast Color > Action in both sighted and early blind (conj.,
8 conjunction analysis); (C) Suprathreshold cluster ($P < 0.05$ FEW corrected) showing greater
9 activity in the rIPS, in sighted compared to early blind, for the contrast Color > Action; (D)
10 Suprathreshold clusters ($P < 0.005$ uncorrected; for illustrative purposes only) showing greater
11 connectivity in the occipital areas of early blind people with the lpMTG (PPI for the contrast
12 Action > Color); (E) Barplot (for illustrative purposes only) showing beta weights derived from
13 PPI analysis, with seed in lpMTG, in sighted (gray) and blind (white), in the right and left
14 middle occipital gyrus (MOG) for the contrast Action > Color (arbitrary unit \pm SEM); (F) Suprathreshold
15 clusters ($P < 0.005$ uncorrected; for illustrative purposes only) showing greater connectivity
16 in the occipital areas of early blind people with the precuneus (PPI for the contrast Color > Action);
17 (G) Barplot (for illustrative purposes only) showing beta weights derived from PPI analysis,
18 with seed in precuneus, in sighted (gray) and blind (white), in the right and left middle
19 occipital gyrus (MOG) for the contrast Color > Action (arbitrary unit \pm SEM).
20

21 **Psychophysiological interactions: The precuneus and lpMTG display similar**
22 **category selectivity across sighted and blind but show different connectivity**
23 **profiles.** Finally, we relied on Psychophysiological Interaction (PPI) analysis (Friston
24 et al., 1997; O'Reilly, Woolrich, Behrens, Smith, & Johansen-berg, 2012) to test
25 whether regions that showed similar categorical preference across groups (lpMTG for

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1 action > color, and the precuneus for color > action) also maintain a similar connectivity
2 profile in both groups. In particular, we tested the hypothesis that posterior occipital
3 areas in the blind could be recruited during conceptual retrieval, and connect with
4 conceptual hubs (Binder et al., 2009) such as the lpMTG and the Precuneus, as a
5 consequence of neural reorganization (Amedi, Raz, Pianka, Malach, & Zohary, 2003;
6 Burton, 2003). With this aim, we selected two ROIs in the left and right middle occipital
7 gyrus (MOG) that are recruited in early blind during high-level conceptual tasks such
8 as language processing and math (Kanjlia et al. 2016; Bedny et al. 2011); and show
9 increased long range connectivity, in early blind, with extra-occipital regions (e.g.,
10 frontal, parietal and ventral temporal cortices) during resting state (Bedny et al. 2011;
11 Kanjlia et al. 2016; Liu et al. 2007; Collignon et al. 2013) and task-based (PPI) analysis
12 (Noppeney, Friston, and Price 2003).

13 PPI with seed in the lpMTG revealed an increase of action-selective functional
14 connectivity in both occipital ROIs of blind people compared to their sighted
15 counterpart (lMOG: $t(33)= 3.59$, $p= 0.02$; rMOG: $t(33)=3.46$, $p=0.026$; Fig 1D & 1E).
16 Similarly, PPI with seed in the precuneus revealed an increase of color-selective
17 functional connectivity in the occipital cortex of blind compared to sighted participants
18 (lMOG: $t(33)= 3.12$, $p= 0.054$; rMOG: $t(33)=4.09$, $p=0.007$; Fig 1F and 1G). Albeit
19 showing a similar activity profile in sighted and blind during conceptual processing, the
20 lpMTG and the precuneus showed a different connectivity profile as a function of early
21 visual deprivation. Such increase in task-based connectivity suggests that occipital
22 areas in early blind, albeit not coding for perceptual similarity as in the sighted, are
23 however active during conceptual retrieval and can be flexibly recruited in interaction
24 with conceptual hubs such as the precuneus and the pMTG.

25

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2 **Discussion**

3 Embodied approaches to conceptual knowledge suggest that concepts are
4 grounded in our sensory and motor experience of the world (Barsalou, 1999; Binder &
5 Desai, 2011). A straightforward hypothesis emerging from these theories is that people
6 that perceive the world in a different way should also have different conceptual
7 representations (Casasanto, 2011).

8 In our study we tested this hypothesis by characterizing the brain activity of
9 sighted and early blind individuals while they rated the perceptual similarity of action
10 and color concepts in fMRI. In particular, we investigated which brain regions encode
11 the perceptual similarity of retrieved concepts using an adaptation paradigm. Results
12 in the sighted group showed that word-pairs referring to similar colors or actions
13 induced repetition suppression in several posterior occipital regions, including areas
14 V3, V4 and V5. In striking contrast, early blind participants did not show repetition
15 suppression in posterior occipital areas but instead showed a greater adaptation for
16 concept similarity in language-related regions, disclosing a different neurobiology of
17 concepts as a function of visual deprivation.

18 Posterior occipital regions are known to encode visual features in the sighted
19 and to be sensitive to visual similarity independently of categorical membership (Bracci
20 and Op de Beeck 2016; Connolly et al. 2012; Kriegeskorte et al. 2008; Naselaris et al.
21 2009). Our data corroborate the hypothesis that these regions are also involved in
22 conceptual retrieval (Borghesani et al., 2016; Fernandino et al., 2015) supporting
23 information related to the visual appearance of objects and events, that is not available
24 to blind people. This result is crucial to support the hypothesis that conceptual retrieval
25 consists, in part, on replay of our perceptual experience (Barsalou, 1999; Harnad,
26 1990).

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1 Since posterior occipital regions represent visual features also during
2 conceptual retrieval (Borghesani et al., 2016; Fernandino et al., 2015; Mitchell et al.,
3 2008), it is therefore expected, as observed in our study, that sighted and blind should
4 show different activity in these regions due to the lack of visual qualia in the blind
5 population. Our results are in line with a previous study showing that relatively anterior
6 regions such as the pMTG and part of the VOTC show a similar functional and
7 connectivity fingerprint in sighted and blind (Wang et al., 2015), whereas this similarity
8 decreases strikingly in more posterior occipital regions (i.e., approximately behind the
9 conventional line that separate the temporal from the occipital lobe; Wang et al. 2015).
10 Actually, the posterior occipital regions showing higher conceptual adaptation in
11 sighted compared to blind in our study tightly overlap with regions showing the lowest
12 functional and connectivity similarity between sighted and blind in Wang et al. study
13 (Wang et al. 2015; Fig. S2).

14 Reduced adaptation in the occipital cortex in our blind participant (compared to
15 sighted) coincides with stronger adaptation in the posterior lateral-temporal cortices
16 (PLTC). Several studies have found that conceptually similar (e.g., dog - wolf) or
17 semantically associated (e.g., dog - leash) words can lead to repetition suppression in
18 PLTC (Wible et al. 2006; Kotz et al. 2002; Bedny, McGill, and Thompson-Schill 2008).
19 Although it is still unclear what level of conceptual knowledge is represented in that
20 region (Bedny, McGill, and Thompson-Schill 2008), there is some agreement that the
21 PLTC stores auditory representations of words, that are connected to distributed
22 semantic representations in the brain (Hickok and Poeppel 2007; Gow 2012; Bedny,
23 McGill, and Thompson-Schill 2008; Mirman et al. 2015). In this framework, the PLTC
24 may work at the interface between wordforms and semantic knowledge (Gow, 2012;
25 Hickok & Poeppel, 2007), and a greater activity in the blind can index a larger use of
26 verbal knowledge in this population (Cattaneo et al., 2008; Crollen et al., 2014).

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1 Directly contrasting different categories (Action Vs Color), independently of
2 within-category similarity, showed instead some commonalities in brain activity across
3 the two groups (Bedny et al. 2012; Noppeney, Friston, and Price 2003; Peelen et al.
4 2014). Both sighted and blind engaged the lpMTG during action processing and the
5 Precuneus during color processing. These regions are located outside of the visual
6 cortex, in polymodal areas, that typically display category-specificity in a format that is
7 at least partially independent from perceptual appearance (Bracci & Op de Beeck,
8 2016; Peelen & Downing, 2017) and largely resilient to visual deprivation (Bedny et al.,
9 2012; Uta Noppeney et al., 2003; Wang et al., 2015).

10 Interestingly, though, psychophysiological interactions (PPI) showed that early
11 visual deprivation changes the connectivity profile of these regions, increasing their
12 functional coupling with occipital regions in the blind. These results suggest that the
13 occipital cortex in early blind is re-organized to extend its integration into conceptual
14 selective networks, highlighting further how visual deprivation impact on the
15 neurobiology of conceptual knowledge. Previous studies have shown that occipital
16 areas in the early blind are recruited for high-level conceptual tasks such as language
17 processing, semantic retrieval and math (Bedny et al. 2011; Kanjlia et al. 2016; Burton,
18 Diamond, and McDermott 2003; Van Ackeren et al. 2018; Crollen et al. 2018; See also
19 Fig. S3 showing general higher activity in the blind occipital cortex during the auditory
20 presentation of words), and that they increase long-range connectivity with frontal and
21 parietal cortices during rest (Bedny et al. 2011; Kanjlia et al. 2016; Liu et al. 2007;
22 Collignon et al. 2013) and inferior temporal cortices during semantic judgments
23 (Noppeney, Friston, and Price 2003). Notably, graph-theoretic metrics of regional
24 cortical thickness covariance found that language and visual regions showed a pattern
25 of merging into shared modules in the blind but not in sighted (Hasson, Andric, Atilgan,
26 & Collignon, 2016). Extending those previous studies, we show here that early blinds

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1 seem to rely on enhanced connectivity between occipital cortices and temporo-parietal
2 conceptual hubs during conceptual processing. Albeit our data remain correlational,
3 they suggest that EBs' occipital regions are not activated independently of other
4 "classic" regions involved in conceptual retrieval, but they instead work in concert.

5 These results suggest that occipital cortices are involved in conceptual retrieval
6 in both sighted and blind, but with different functions and probably at different levels of
7 representation. Occipital areas may support sensorimotor simulations of visual
8 features during conceptual retrieval in the sighted, showing adaptation for concepts
9 that refer to visually similar objects or events; on the other hand, in the blind, occipital
10 cortices do not encode perceptual similarity, but may be re-organized to engage in
11 more general processes related to conceptual retrieval (albeit these processes need
12 to be better specified; see for instance, Bedny 2017; Van Ackeren et al. 2018).

13 Outside the posterior occipital cortex, we found that the posterior portion of the
14 right IPS showed a stronger preference for color trials in the sighted compared to the
15 blind. The IPS is known to be involved in the perception of color (Beauchamp et al.,
16 1999; Cheadle & Zeki, 2014; Zeki & Stutters, 2013) as well as other visual features
17 (Grill-Spector, 2003; Swisher, Halko, Merabet, McMains, & Somers, 2007; Xu, 2007),
18 and its anatomical position make it a good candidate to work at the interface between
19 perceptual and conceptual representations (Cheadle & Zeki, 2014). In particular, it
20 seems to be crucial for retrieving perceptually-based categorical knowledge (Cheadle
21 & Zeki, 2014; Zeki & Stutters, 2013). Indeed, the peak of color-specific activity that we
22 found (peak coordinates: 33, -43, 35) is very close to the color-specific rIPS area found
23 by Cheadle & Zeki (2014; peak coordinates: 30, -39, 45). The lack of visual input in
24 blind people prevents the formation of perceptually-driven color representations, which
25 may limit the contribution of the IPS during the retrieval of color knowledge. This is not
26 the case for action representation, for which perceptual knowledge can be more easily

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1 compensated by other senses (e.g., touch, audition) in the blind. The distinct impact of
2 blindness on the broader categorical responses to action and colors again highlight
3 how visual experience may selectively shape the neurobiology of conceptual
4 representations, even in putatively multimodal areas of the brain.

5 From a broader theoretical point of view, the results of this study are in line with a
6 hierarchical model of conceptual representations based on progressive levels of
7 abstraction (Barsalou, 2016; Binder, 2016; Binder et al., 2016; Fernandino et al., 2015;
8 A. Martin, 2015). At the top of the hierarchy, multimodal representations may co-exist
9 with purely symbolic ones organized in a linguistic/propositional code (Mahon &
10 Caramazza, 2008). This level of representation can account for the obvious fact that
11 congenitally blind people can think about colors and their perceptual properties
12 (Barilari, de Heering, Crollen, Collignon, & Bottini, 2018; Marmor, 1978) although they
13 cannot simulate vision. On the other hand, modality-specific simulation in sensory
14 areas (e.g. visual, auditory, somatosensory), as the one highlighted by our adaptation
15 analysis, may become central in deeper and more deliberate stages of conceptual
16 processing, providing situated, specific and sometimes imaginistic representations,
17 and eventually supporting the subjective experience of knowing providing the
18 phenomenological qualia of conscious thinking (Binder et al., 2016; Koch, Massimini,
19 Boly, & Tononi, 2016).

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