# Insights into the origins of knowledge from the cognitive neuroscience of blindness

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Children learn about the world through senses such as touch, smell, vision, and audition, but they conceive of the world in terms of objects, events, agents, and their mental states. A fundamental question in cognitive science is how nature and nurture contribute to the development of such conceptual categories. What innate mechanisms do children bring to the learning problem? How does experience contribute to development? In this article we discuss insights into these longstanding questions from cognitive neuroscience studies of blindness. Despite drastically different sensory experiences, behavioural and neuroscientific work suggests that blind children acquire typical concepts of objects, actions, and mental states. Blind people think and talk about these categories in ways that are similar to sighted people. Neuroimaging reveals that blind people make such judgements relying on the same neural mechanisms as sighted people. One way to interpret these findings is that neurocognitive development is largely hardwired, and so differences in experience have little consequence. Contrary to this interpretation, neuroimaging studies also show that blindness profoundly reorganizes the visual system. Most strikingly, developmental blindness enables "visual" circuits to participate in high-level cognitive functions, including language processing. Thus, blindness qualitatively changes sensory representations, but leaves conceptual representations largely unchanged. The effect of sensory experience on concepts is modest, despite the brain's potential for neuroplasticity.

*Keywords*: Conceptual development; Innateness; Experience; Blindness; Concepts.

... imagine a child, growing up in a certain city, born blind, but otherwise intelligent and well endowed, with a sound memory and an apt mind. Through his remaining channels of perception he will get to know the people as well as all sorts of animals and objects, and the streets and alleys, houses and markets—eventually well enough to walk through the city without a guide, recognizing at once everyone he meets. But colours, and colours alone, he will know only by descriptive explanation and ostensive definition. Suppose after he had come this far, his eyesight were restored and he could see. He would walk all through the town finding nothing in contradiction to what he had believed, nor would anything look wrong to him. The colours he encountered would conform to the guidelines that had been sketched out for him. Still there would be two great changes, the second dependent on the first: first the daybreak on a new visual world, and second, his great joy.
(from *Hayy Ibn Yaqzan*, by Ibn Tufayl, 12th century Andalusian Islamic scholar)

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Children learn about the world through sensations such as seeing shapes, feeling softness, and listening to sounds. Yet children think (and talk) in abstract terms that go way beyond sensory experience. Children categorize events as instances of *running*, whether the running is done by a boy, a turtle or a cheetah; and call running something different when it's done for the purpose of *chasing*, *racing*, or *escaping*. Children can distinguish between *falling* and *jumping* into the swimming pool and between *doubting* and *hoping* that they will get ice cream before dinner. Perhaps the most canonical human behaviour, language, is a feat of abstraction, both in the conceptual categories it picks out and the grammatical rules that govern its use. A fundamental question in cognitive science is how nature and nurture contribute to the development of such abstract representations. What innate learning mechanisms or conceptual "cores" do children bring to the problem of cognitive development (e.g., Spelke, 1998)? How does experience enable children to distinguish between *falling* versus *jumping*, *doubting* versus *hoping?*

Understanding how experience contributes to cognition is a formidable task. First, most people share the vast majority of their genes and important aspects of their environment. Almost all children experience sounds, sights, gravity, motion, language, and social interactions with other humans. Our shared nature and nurture make it difficult to separate the contributions of intrinsic biological constraints and experience, and to disentangle correlated dimensions of experience from each other. Individuals who grow up with *atypical* experiences provide rare insights into the causal mechanisms that shape cognition (Benzaquen, 2006; Gleitman & Newport, 1995).

Blindness in particular has long been a window into the developmental origins of the mind (Berkeley, 1709/1732; Hobbes, 1641/1984). Unlike sighted children, blind children do not see colours or faces, they do not follow the gaze of others, they do not see mountains, elephants, or a flickering fire, and the fact that two people are hugging near by is largely inaccessible to them. Blind infants have limited opportunities to observe objects, actions, and the perceptual states of other people. They have no access to facial expressions or eye gaze, and do not share first-person experiences of seeing with the sighted people around them. How does conceptual development differ, under these circumstances? How do blind children develop concepts of objects, actions, seeing, and thinking, and what are these concepts like in blind adults?

Cognitive scientists have investigated these philosophical puzzles by quantitatively studying the behaviour of blind individuals (Iverson & Goldin-Meadow, 1997; Landau, Gleitman & Spelke, 1981; Landau, Spelke & Gleitman, 1984; Shepard & Cooper, 1992). These studies have yielded illuminating, and sometimes surprising insights into the human mind. Most notably, aspects of cognition that were thought to depend heavily on vision, such as spatial reasoning, have turned out to develop quite typically in the absence of sight (Landau et al., 1981, 1984). Recently, the methods of cognitive neuroscience have opened up new opportunities to study the relationship between visual experience and neuro-cognitive development.

In this review we highlight insights from these neuroscientific studies of blindness. Studies of the neurobiology of concepts in blind people test some long held (and recently revived) claims about the sensory origins of cognition. Since the sensory experience of blind and sighted people is drastically different, does the neurobiology of concepts also differ in these populations? Augmenting behavioral findings, measures of brain function provide insights into whether blind and sighted people rely on similar cognitive mechanisms to solve the same behavioural tasks, not just "talking the talk". We centre our discussion on studies of several conceptual categories that are believed to depend heavily on vision: objects, actions, and perceptual states. We then consider the implications of these studies for theories on the organization of conceptual knowledge.

Studies of blindness also offer insights into how the mind is implemented in the brain. In particular, blindness offers a window into how nature and nurture contribute to human brain

development. Congenital blindness causes a dramatic change to the typical developmental input of visual\cortex. Studies of the visual cortex in blind individuals thus offer an opportunity to explore the limits of neuroplasticity in the human brain. As we discuss below, these studies have begun to uncover how intrinsic constraints interact with experience during human brain specialization.

We begin by reviewing evidence of neuroplasticity in the visual system of blind individuals and then turn to studies of the neurobiology of concepts. We then juxtapose the effects of blindness on the visual system to its effects on conceptual systems. To foreshadow, while studies of the visual system in blind individuals reveal dramatic functional reorganization, studies on the neurobiology of concepts reveal resilience to blindness. The strikingly different effects of blindness on perceptual and conceptual systems inform our understanding of the distinctive nature and origins of such systems.

## INSIGHTS INTO NATURE/ NURTURE QUESTIONS FROM NEUROPLASTICITY IN THE VISUAL SYSTEM

To what degree are the cognitive functions of neural circuits intrinsically constrained, even before receiving input from the environment (innate)? Prior to experience, human cortical areas differ from each other in the distribution and proportion of neuronal types as well as connectivity to other neural circuits. Do such neuroanatomical features ingrain a particular cognitive function (e.g., visuospatial discrimination, language, working memory)? Conversely, can lifetime experience qualitatively change the cognitive capacity of neural tissue? Studies of occipital cortex in blind individuals pit strong innate constraints against large-scale changes in experience.

The mammalian occipital cortex is believed to have evolved for vision. Comparative studies of brain anatomy across species suggest that those mammals that rely more on vision also have more elaborated occipital circuits (Barton, 2007; Kaas, 2008). The occipital cortex is anatomically tailored to the demands of sight: Primary visual cortex ("V1") has a disproportionately thick input layer (IV) and is massively dominated by input from the visual nucleus of the thalamus (the lateral geniculate nucleus). In sighted humans the visual system has a highly predictable functional organization both within visual cortical areas (e.g., retinotopy) and across cortical areas (e.g., motion, colour, object selectivity). Such consistency suggests the existence of strong innate biases. If any structure were to be resilient to changes in environmental input, it might be the visual system.

On the other hand, if experience could effect brain organization, total blindness should do so since it constitutes a massive change to typical developmental input. By contrast, most experiential changes in higher-cognitive domains are subtler, e.g., variation in socioeconomic status, reduced access to language due to deafness, or experimentally induced training. In all these cases typical experience is altered or reduced rather then removed entirely. Studies of total blindness therefore test the limits of cortical flexibility in the context of extreme changes in the environmental input. If the cognitive function of neural circuits is innately determined, absence of vision might lead occipital cortex to simply atrophy. By contrast, if neural circuits have the capacity to change function in the face of different input, the visual system of blind people would be likely to show this plasticity: losing visual functions, but possibly gaining other functions. If visual circuits do acquire new functions, we can ask how cognitively or computationally similar these functions are to vision?

Fifty years of neuroscientific research, in both humans and nonhuman animals, provides clear evidence for functional change in the visual system (Hubel & Wiesel, 1970; Wiesel & Hubel, 1963). First, blindness leads "visual" circuits to support vision less optimally. Removing visual input even temporarily during development leads to disorganization and loss of visual functions

in the deprived cortex, and to corresponding visual deficits (Levin, Dumoulin, Winawer, Dougherty & Wandell, 2010; Wiesel & Hubel, 1963, 1965). For example, dark-reared ferrets do not develop classic direction selectivity in visual cortex (Li, Fitzpatrick, & White, 2006). In humans, temporary absence of pattern vision early in life (e.g., due to cataracts) leads to reduced acuity and persistent deficits in high-level vision even many years later (Fine et al., 2003; Levin et al., 2010; Maurer, Lewis, & Mondloch, 2005; Ostrovsky, Andalman & Sinha, 2006; Putzar, Goerendt, Lange, Rosler, & Roder, 2007). Just a few months of lost vision during infancy causes enduring impairments in adult face perception (Le Grand, Mondloch, Maurer, & Brent, 2003, 2004). Blind individuals who recover vision as adults (i.e., following years of blindness) have even more dramatic deficits and fail to show typical (category-specific) neural responses to faces and objects in visual cortex (Fine et al., 2003).

Second, in addition to loss of visual function, early blindness also enables occipital cortex to take on nonvisual functions. Animals who are deprived of vision early in life develop responses to touch and sound in occipital regions that would normally respond exclusively to vision (Kahn & Krubitzer, 2002; Rauschecker, 1995). Similarly, early neuroimaging studies with humans showed that occipital regions of blind people respond to touch and sound (Kujala et al., 1995; Uhl, Franzen, Lindinger, Lang & Deecke, 1991). For example, occipital regions are active when blind, but not sighted, individuals read Braille (Sadato et al., 1996; Uhl et al., 1991). Furthermore, transient disruption of occipital cortex by transcranial magnetic stimulation (TMS) impairs blind people's ability to recognize Braille letters by touch (Cohen et al., 1997; Hamilton, Keenan, Catala & Pascual-Leone, 2000), suggesting that crossmodal responses in the visual system are functionally relevant, not epiphenomenal.

Traditionally, these tactile and auditory responses in the visual system have been termed "crossmodal plasticity" because transfer of function is believed to occur from one sensory modality to another (e.g., from vision to touch) while preserving the underlying cognitive function (e.g. Merabet et al., 2004). For example, like vision, Braille reading requires fine-grained spatial discrimination (Sadato et al., 1996). Thus, although the modality of input to "visual" cortex is changed, the underlying cognitive function of visual cortex (i.e. spatial perception) might remain the same (Collignon et al., 2011). There are a number of similar examples where plasticity appears to preserves elements of the original cognitive function. For instance, the middle temporal complex (MT/MST) typically plays an important role in perception of visual motion (Dubner & Zeki, 1971; Tootell et al., 1995a, 1995b; Zeki, 1974). In congenitally blind individuals, this brain region responds to auditory motion (Bedny, Konkle, Pelphrey, Saxe, & Pascual-Leone, 2011b; Poirier et al., 2006; Saenz, Lewis, Huth, Fine & Koch, 2008; Wolbers, Zahorik & Giudice, 2011). In the cases of Braille and auditory motion, blindness changes the sensory modality that drives occipital circuits, but the underlying cognitive function may be preserved (Pascual-Leone, Amedi, Fregni & Merabet, 2005; Pascual-Leone & Hamilton, 2001; Rauschecker, 1995).

Other cases of plasticity provide clear examples of functional change that is more dramatic than crossmodal transfer. The most striking example is the acquisition of linguistic functions by occipital cortex. In most humans, the capacity for language depends on a neural system of left-lateralized brain regions in prefrontal and temporoparietal cortex. Like the visual system, the neurobiology of language is often resilient to environmental change. Children who grow up in different cultures and speak different languages (including both aural languages and sign languages) go on to develop similar fronto-temporal language systems (Bellugi, Poizner & Klima, 1983; Chee et al., 1999a; Chee, Tan & Thiel, 1999b). By contrast, adults who are blind from birth engage occipital (visual) cortex during language processing, in addition to classic language areas (Bedny, Pascual-Leone, Dodell-Feder, Fedorenko & Saxe, 2011c; Burton, Diamond & McDermott, 2003; Roder, Stock, Bien, Neville & Rosler, 2002).

Left-lateralized areas in the "visual" cortex respond not only during Braille reading (Buchel, Price, Frackowiak & Friston, 1998; Burton et al., 2002a; Hamilton & Pascual-Leone, 1998; Sadato et al., 1996), but also while blind individuals listen to aural speech (Amedi, Raz, Pianka, Malach & Zohary, 2003; Bedny et al., 2011c; Burton & McLaren, 2006) and covertly generate (i.e. think of) words (Amedi et al., 2003; Burton, Snyder, Diamond & Raichle, 2002b). Occipital cortex activity during language tasks is related to language processing specifically, and not to nonlinguistic aspects of verbal tasks such as general task difficulty or language-related imagery. Left occipital areas respond more during linguistic tasks than to difficult nonlinguistic perceptual and working memory tasks (Bedny et al., 2011c; Bedny, Pascual-Leone, Dravida & Saxe, 2011d). Various lines of evidence demonstrate that occipital activity during verbal tasks does not reflect spontaneous spatial imagery (Lakoff & Nunez, 2001). First, both in sighted and congenitally blind individuals, explicit imagery and language comprehension depend on distinct neural circuits (Vanlierde, De Volder, Wanet-Defalque, & Veraart, 2003). Second, the occipital response to sentences is not correlated with imagery ratings (Bedny, Dufour, Dravida, & Saxe, 2010) and is observed to linguistic stimuli that do not support visual imagery, including abstract words and Jabberwocky sentences (Amedi et al., 2003; Bedny et al., 2011c; Roder et al., 2002).

Like classic language areas, occipital regions in blind adults are sensitive to high-level linguistic information (i.e., compositional sentence structure and word meanings). Occipital brain regions respond more to Jabberwocky (containing compositional structure but no content words), and more to lists of words (content words with no compositional structure) as compared to lists of nonwords (low in both compositional structure and word meanings; Bedny et al., 2011c) (Figure 1). There is also evidence that occipital areas respond more to syntactically noncanonical than canonical sentences (Roder et al., 2002).

Even in the absence of a task (i.e., while simply resting), occipital activity in blind individuals is correlated with activity in prefrontal language areas (Bedny et al., 2011c; Liu et al., 2007; Watkins et al., 2012).

Finally, as in the case of Braille reading, occipital responses to language appear to be functionally relevant: TMS applied to the occipital pole leads to verb-generation errors in blind but not sighted individuals (Amedi, Floel, Knecht, Zohary & Cohen, 2004). Together these findings suggest that the visual system takes on language processing capacities as a result of blindness. These data imply that experience can induce human brain regions to change functions not only across sensory modalities, but also across cognitive domains (i.e., from vision to language).

While human cortical circuits appear to be highly flexible in the cognitive functions they can support, this flexibility declines and changes with age. Responses to nonvisual stimuli in occipital circuits are more robust and more widespread in people who are blind from birth (Burton et al., 2002a), and are also differentially localized in congenitally versus late blind people (Bedny et al., 2011d; Buchel et al., 1998; Burton et al., 2002a).

Age of blindness onset also affects which cognitive functions occipital circuits take on. While the visual system is active during verbal tasks (e.g., Braille reading, verb generation) in both late and congenitally blind people (Burton et al., 2002a), occipital regions contribute to language processing *per se* only in congenitally blind people. These differences in functional plasticity between late and congenitally blind people depend on the age of blindness onset, not the years of blindness. Even after decades of blindness, occipital areas respond equally to difficult linguistic and nonlinguistic tasks in late blind people (Bedny et al., 2011d). Also, TMS to the occipital pole impairs Braille reading only in congenitally blind individuals (Cohen et al., 1997). These data suggest that blindness during development specifically enables occipital circuits to participate in language processing.

We have recently begun studying the time-course and mechanism of this language-related plasticity by working with blind children. Preliminary findings suggest that occipital cortex plasticity for language occurs during early
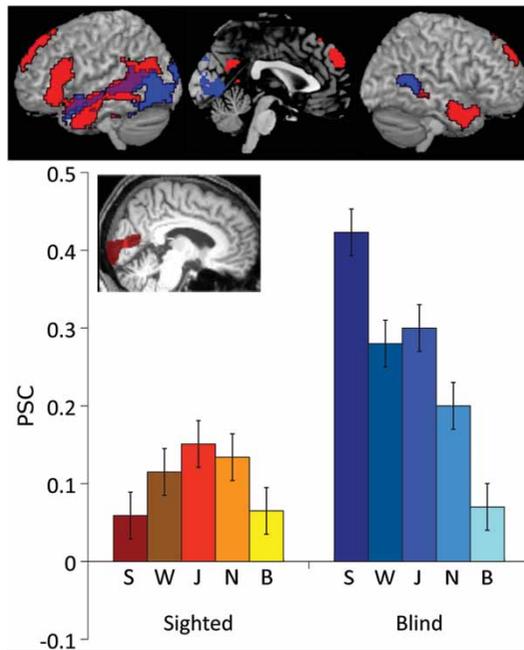
**Figure 1.** *Neural activity during sentence comprehension in sighted and blind individuals. Top panel shows results of a whole-brain analysis comparing sentences to backwards speech in sighted (red) and blind (blue) people. Whole-brain random-effects results are overlaid on a standardized template (corrected for multiple comparisons, $p < .05$). Bar charts show percent signal change (PSC) in pericalcarine cortex (approximate anatomical location of V1) while listening to sentences (S), word lists (W), Jabberwocky (J), nonword lists (N) and backwards speech (B). (For details see Bedny et al., 2011c.). To view a colour version of this figure, please see the online issue of the Journal.*

childhood. Occipital responses to language emerge in blind children by four years of age and appear to be independent of Braille learning (Bedny et al., 2012). These data suggest that occipital cortex takes on language functions during development, and possibly during language acquisition.

In sum, early blindness enables brain regions that evolved for vision to develop multiple nonvisual functions, including multimodal sensory responses and even high-level language functions. In the visual cortex innate predispositions coexist with the potential for large-scale experience-based change. These findings imply that developmental experience can qualitatively change the function of neural tissue across disparate cognitive domains. During development cortical areas are pluripotent: the same circuits can support both basic sensory and abstract cognitive functions.

Since experience in general and blindness in particular has the potential to reorganize neural systems, we can next ask how blindness affects the neurobiology of concepts. If sensory experience and concepts are tightly linked, changes to sensory systems should carry forward to conceptual representations. Conversely, preserved conceptual representations in the face of blindness would provide evidence for decoupling between sensation and concepts.

## CONCEPTS AND BLINDNESS

### The potential contribution of neuroscientific data to theories of concepts

Philosophers have long wondered what the concepts of blind people might be like. Many have

concluded that the concepts of blind people must be very different from the concepts of sighted people, or at least missing a crucial piece (Hume, 1739/1978). Thomas Hobbes likened a blind person's knowledge of fire to a sighted person's knowledge of God (Hobbes, 1641/1984). The Anglo-Irish Empiricist George Berkeley similarly argued that blind people have drastically different concepts of everyday objects (Berkeley, 1709/1732). More recently, the psychologist Thomas Cutsforth wrote about the "unreality of words to the blind", asserting that terms such as "look" and "see" are meaningless to congenitally blind individuals and discouraging the use of such words by blind children (Cutsforth, 1932). These intuitions about blindness are founded on the premise that concepts are tightly linked to their perceptual origins. Similar empiricist commitments have been central to modern cognitive and neuroscientific theories (Allport, 1985; Paivio, 1971; Warrington & Shallice, 1984), including recent "embodied" theories of cognition (Barsalou, 1999; Gallese & Lakoff, 2005; Glenberg, 1997; Lakoff & Johnson, 1980; Prinz, 2002, 2005; Pulvermuller, 1999; Wilson, 2002). Since the sensory experience of blind people is very different from the experience of sighted people, these theories also predict that the concepts of blind people should be very different.

In sum, one view of conceptual development and organization is that concepts are largely sensory and thus modality-dependent. On this view, "visual" concepts can only be acquired normally through vision, and blind people should have large gaps in their concepts, compared to the concepts of sighted people. These gaps are most likely for concepts that in sighted people are putatively highly visual: concrete objects, actions, and experiences that specifically involve vision, such as seeing.

While modern empiricist theories are consistent with modality-dependence, they are also consistent with a weaker prediction, which we call the modality-flexible hypothesis. Embodied concepts must be sensory, but they need not be visual (Barsalou, 1999; Gallese & Lakoff, 2005; Glenberg, 1997; Lakoff & Johnson, 1980; Prinz,

2002; 2005; Pulvermuller, 1999; Wilson, 2002). Blind people could efficiently compensate for the absence of vision with images from other modalities. Concepts that sighted people acquire through vision and represent as visual images (e.g., *blue*, *bounce*, and *see*), could be acquired through touch or audition and represented as tactile and/or auditory images in the minds of people who are blind (Gallese & Lakoff, 2005; Meteyard, Cuadrado, Bahrami & Vigliocco, 2012). On this view, blind and sighted people might have similar knowledge and similar behaviour, but with different conceptual organization.

The third view we will consider here is the modality-invariant hypothesis. According to this proposal, in addition to knowing what things look like, people process a vast store of abstract conceptual information that allows them to make inferences, to categorize, and to communicate with others. On this view many concepts are largely abstract and modality-invariant, in both sighted and blind people. For example, action concepts might include abstract information about duration, causal structure, and agent intentions as well as spatial information, such as motion path, that is not modality-specific. This kind of conceptual information is modality-invariant in that the same information could just as well be acquired through vision, audition, or touch without any change to the underlying representations. This information might be acquired via innate "core" learning mechanisms that evolved for acquiring these abstract categories (Carey, 2009; Spelke, 1998; Spelke & Kinzler, 2007). Alternatively, these representations could be acquired by observing or inferring abstract structure from the environment (e.g., by observing causal interactions, intentional actions), and through language. For example, a child might learn that a giraffe is a type of animal that eats leaves either by hearing mom talking about giraffes or seeing a giraffe eating leaves in a zoo. Auditory versus visual means of learning this information may have no representational consequences. Similarly, learning what it means to see either by hearing others talk about seeing or by having first-person

experiences of seeing might lead to qualitatively similar concepts.

The modality-dependent, modality-flexible and modality-invariant hypotheses outlined above serve as anchor points for our discussion of concepts in blind individuals. We end this section of the paper with some qualifications of these idealized theoretical position. The available behavioural and neuroscientific data on blindness contribute powerful evidence for disentangling these three positions. Decades of behavioural research weighs in against the modality-dependent view. The linguistic and reasoning behaviour of congenitally blind, and even deaf–blind individuals is largely similar to that of sighted people (Chomsky, 1986). Conceptual development is preserved in higher-cognitive domains that were thought to depend on vision (Iverson & Goldin-Meadow, 1997; Landau et al., 1981, 1984; Marmor & Zaback, 1976; Zimler & Keenan, 1983). Perhaps most strikingly, concepts of seeing are not hopelessly out of reach of blind adults and children (Bigelow, 1992; Landau & Gleitman, 1985; Peterson, Peterson, & Webb, 2000). Young blind children use terms such as "look" and "see" systematically to refer to visual perception in sighted people (and to tactile perception in themselves). They use colour words appropriately, to refer to a specific class of related perceptual qualities that cannot be perceived by touch but can be perceived through vision (Landau, 1983; Miller, 1983; Rosel, Caballer, Jara, & Oliver, 2005).

On the other hand, it can be difficult to distinguish between the modality-flexible and modality-invariant hypotheses using behavioural data alone. To illustrate this point, consider the conceptual category of colours. Blind children have no perceptual access to colour; there is no way to perceive colour other than through sight. Despite this, when blind adults are asked to make similarity judgements based on colour words, their ratings reflect a similarity space that resembles the Newtonian colour wheel (Marmor, 1978; Shepard & Cooper, 1992). Blind children begin to produce colour adjectives at approximately the same time as sighted children. Four-

year-old blind children use colour names to refer to perceptual qualities of objects that cannot be felt by touch; and know that while concrete objects can all have colours, events and abstractions cannot have colours (Landau & Gleitman, 1985). By eight to 13 years of age blind children can name the colours of common objects (Connolly, Gleitman, & Thompson-Schill, 2007 for evidence in adults; Mills, 1983). There is also anecdotal evidence that blind children know other information about colours. A blind eight-year-old girl that recently visited our lab asked what the colour of her chair was. When told that the chair was blue, she politely asked if she might have a red or pink chair instead, "since blue is a boy colour".

On the other hand, there is also behavioural evidence that colour knowledge of blind people is not identical to that of sighted people. While the similarity judgements of all sighted people yield a Newtonian colour wheel, the ratings of blind people vary across individuals; some blind adults make judgements that do not reflect the Newtonian colour wheel (Shepard & Cooper, 1992). Blind people also tend to neglect colour information when making decisions about objects. Even when they can name the colours of common objects (e.g., fruits and vegetables), blind people do not use colour information to decide how similar a "banana" and a "lemon" are to each other (Connolly et al., 2007).

Behavioural evidence regarding colour concepts can thus be interpreted in two ways. The evidence that blind people on average acquire rich and accurate knowledge about colours, including associations to objects and cultural categories, demonstrates that even colour concepts can be acquired through non-sensory mechanisms, such as language. It seems possible that both blind and sighted children develop amodal representations of colour, consistent with the modality-independent hypothesis. Such representations might include information about how colour is perceived, gender correlations, and even the similarity of colours to each other. On the other hand, evidence that blind people's colour similarity space is heterogeneous and relatively underutilized

supports the proposal that concepts are qualitatively distinct in blind and sighted people. In sighted people, colour concepts may be largely visual images, whereas for blind people they may be represented by analogy to other sensory modalities or in some other compensatory format, consistent with the modality-flexible hypothesis.

Even in cases where the behaviour of blind and sighted people is identical, it is still possible that different formats of representation are at play. For example, like sighted people, congenitally blind people take a longer time to perform mental rotation tasks as the angle of rotation between the two objects increases (Marmor & Zaback, 1976). This could be because both blind and sighted people are relying on a modality-independent spatial representation or because blind people use tactile representations where sighted people rely on visual representations (modality-flexible hypothesis). When the behaviour of blind and sighted people is generally similar, how can we tell whether blind and sighted people are relying on the same cognitive mechanisms, or whether blind people are efficiently compensating with alternative sensory modalities?

Measurements of neural activity can weigh in on the interpretive ambiguities left by behavioural findings. Information from different sensory modalities (e.g., vision versus touch) and different domains of knowledge (e.g., language versus space) is represented in distinct parts of the human cortex. As a result, the modality-flexible and modality-invariant hypotheses make different predictions for neural data. According to the modality-flexible view, for concepts whose organization is based on the sensory modality of acquisition, blind and sighted people achieve similar behavioural performance by depending on different formats of representation. Since we can distinguish brain regions that are dominated by different sensory modalities (e.g., auditory cortex and visual cortex), we can use neural data to ask whether blind and sighted people rely on similar or different cognitive mechanisms to solve the same behavioural tasks. In some cases, we can even make specific predictions about exactly which brain regions should be involved for each

population (more on this below). We can also look for effects of blindness on the functional selectivity of those neural circuits that support conceptual tasks. If concepts are sensory, then blindness should change the functional profile of conceptual brain regions, as we know it changes the functional profile of visual brain regions. For concepts whose organization is independent of modality and structured around abstract features, blind and sighted people should achieve similar behavioural performance by appealing to the same neural mechanisms.

## Concepts of objects and actions in blind individuals: Behavioural evidence and neural predictions

There is little doubt that sighted infants initially rely heavily on vision to learn about concrete objects and actions (Smith & Heise, 1992). Within the first year of life children use shape, pattern, and colour to individuate objects in their environment (Wilcox, 1999). Eleven-month-old infants use visual motion to parse actions and events along conceptually relevant boundaries (Baldwin, Baird, Saylor, & Clark, 2001) and infants infer intentional information based on visual cues (Woodward, 1998).

Blind children's experiences with objects and actions differ from those of sighted children both qualitatively and quantitatively. Qualitatively, blind infants learn about their environment through different sensory modalities—touch and audition rather than vision. This change in input modality also makes some kinds of information more accessible than other kinds. For example, perceptual information about texture and weight is more salient, whereas information about silhouettes, shape, and colour is less salient. Quantitatively, blind children also have less overall access to information about objects and actions in their environment. As a result, there is some evidence that blind children's behaviour is initially less directed towards external objects and events than the behaviour of sighted children. Blind children are delayed in reaching for distant objects (Adelson & Fraiberg, 1974). When blind

children first begin to talk, they refer to other people's actions less frequently than to their own actions (compared to age-matched sighted children) (Andersen, Dunlea & Kekelis, 1984; Bigelow, 1987; Dunlea, 1989).

All three hypotheses about conceptual organization outlined above can be formulated specifically, regarding concepts of objects and events. First, if such concepts require vision for normal development, then blind children should be substantially (and in some cases, possibly permanently) delayed in acquisition of typical concepts of objects and actions (modality-dependent hypothesis) (Andersen et al., 1984; Cutsforth, 1932; Dunlea, 1989). Second, the modality-flexible hypothesis predicts that while sighted children's concepts are derived from visual experience, blind children efficiently compensate with sensory information from other modalities. For example, where sighted children acquire object concepts in the form of visual images of shape, blind children might represent shape information in a tactile format. Third, the modality-invariant hypothesis predicts that object and action concepts have key amodal components that are invariant with regard to modality of input. If so, blind children should acquire the very same concepts of objects and events as do sighted children.

Again, behavioural evidence clearly advocates against the modality-dependent hypothesis. Blind children's acquisition of words for objects and actions is largely unaffected (Johnson & Newport, 1989; Landau, 1983; Landau & Gleitman, 1985; Perez-Pereira & Castro, 1992; Urwin, 1983). Production of first words is only slightly, if at all, delayed (Bigelow, 1987; Landau & Gleitman, 1985; Urwin, 1983) and these first words consist mostly of names of objects and actions (Bigelow, 1987). By three years of age, blind children's lexical and grammatical development is largely indistinguishable from the development of sighted children (Landau & Gleitman, 1985).

The behavioural data leave open the two remaining hypotheses: that blind children compensate with sensory information from other modalities (modality-flexible hypothesis) or that

concepts of objects and actions are invariant with regard to the sensory-modality of learning in both blind and sighted children (modality-independent hypothesis). Neuroscienctific studies of concepts in blind individuals can help distinguish between these possibilities. In particular, since there are specific brain regions that have been hypothesized to support object and event concepts respectively, we can ask how the development of these brain regions is affected by blindness.

## Neural basis of object concepts in blind individuals

Knowledge of objects, such as animals and artifacts, is thought to depend in part on regions of the ventral temporal cortex. These areas are active when people listen to object names, and damage to this part of the brain causes deficits in knowledge about everyday objects (Caramazza & Shelton, 1998; Goldberg, Perfetti & Schneider, 2006; Hsu, Frankland & Thompson-Schill, in press; Kan, Barsalou, Solomon, Minor & Thompson-Schill, 2003; Martin, 2007; Simmons et al., 2007; Thompson-Schill, 2003; Tranel, Damasio & Damasio, 1997; Warrington & McCarthy, 1987; Warrington & Shallice, 1984). Within the ventral temporal cortex, there are also brain regions that support visual perception of objects such as animals, faces, and tools (e.g., Grill-Spector, 2003; Riesenhuber & Poggio, 2002). These brain regions are thought to represent modality-specific visual information about object shape, colour, and size. One interpretation of these findings is that ventral temporal representations of objects consist entirely or primarily of modality-specific visual images, and these same images are recruited as parts of the meanings of object words (Barsalou, Kyle Simmons, Barbey, & Wilson, 2003; Beauchamp & Martin, 2007; Martin, 2007; Pecher, Zeelenberg, & Barsalou, 2004; Pulvermuller, 1999; Pulvermuller & Hauk, 2006). This interpretation is consistent with the modality-dependent and modality-flexible hypotheses.

A related, but distinct proposal is that ventral temporal representations of object concepts are not themselves visual images but are derived from visual images. On this view, conceptual brain regions in the ventral temporal cortex are situated near visual brain regions because of their sensory history (Allport, 1985; Thompson-Schill, 2003). For example, because sighted people learn about objects primarily through vision, they might develop representations of object concepts near visual circuits involved in perceiving shape and colour.

Both of these interpretations of ventral temporal responses to objects in sighted people predict that these responses should be absent or at least organized differently in congenitally blind adults. When a blind person understands the word "giraffe", they cannot be recalling a visual image of a giraffe's shape. Contrary to this prediction, several studies have found ventral temporal responses to object concepts in congenitally blind adults (Noppeney, Friston, & Price, 2003). For example, Mahon and colleagues presented blind and sighted people with names of tools (e.g., hammer), non-manipulable artifacts (e.g., desk) and animals (e.g., giraffe) (Mahon, Anzellotti, Schwarzbach, Zampini & Caramazza, 2009). Participants made judgements about whether sequentially presented objects are similar in size. The neural pattern of response to animals and tools was similar in blind and sighted individuals. First, blind and sighted people both showed ventral temporal responses to both categories of objects. Second, the pattern of ventral temporal responses to tools versus animals was similar in blind and sighted people: Both groups showed a more medial response to tools and a more lateral response to animals (for converging evidence with nonverbal materials see Pietrini et al., 2004). Overall, there were no differences in the brain regions recruited for understanding object names (and making size judgements) in blind and sighted people. These findings suggest that some object-responsive regions in ventral temporal cortex do not depend on vision for normal development (see also Mahon, Schwarzbach, & Caramazza, 2010 for further evidence of preserved neurobiology of tool concepts).

One interpretation of these findings is that one set of regions in the ventral temporal cortex stores modality-independent information about objects (e.g., spatial shape representations or abstract information about animal ontogeny), and another, distinct group of regions stores modality-specific images of what objects look like. Within the modality-independent regions, the neural distribution of object information might not depend on sensory modality; instead, organization might depend on factors such as the relevance of function to category membership (Mahon et al., 2007). If so, we can infer that when people make semantic decisions based on object labels, they do so relying on modality-independent representations and not the visual images (which is why blind and sighted people show the same patterns of activation in such tasks). Visual images could still be retrieved for some detailed judgements about appearance (e.g., is a carrot darker than a stop sign?) (Thompson-Schill, 2003) but not, for example, as an automatic part of word comprehension. Seen in this light, studies of the neurobiology of objects provide evidence for the modality-invariant view (see below for a discussion of possible theoretical ambiguities).

However, these data remain open to alternative interpretations that are consistent with the modality-flexible view (Mahon et al., 2009). Ventral temporal object representations might be dominated by visual information in sighted people and compensated for by tactile or auditory information in blind people (Mahon et al., 2009; Meteyard et al., 2010). The similar patterns of neural activity in sighted and blind adults could reflect crossmodal plasticity, via which auditory and tactile information can come to activate typically visual areas (Sadato et al., 1996). For example, developmental blindness could strengthen weak tactile afferents to ventral temporal cortex. If the ventral temporal cortex additionally has some innate predisposition to represent shape information, it might then develop tactile shape representations in blind individuals (Amedi et al., 2007; Pascual-Leone & Hamilton, 2001) just as MT/MST represents motion from

auditory input. Object representations could still be composed of sensory images in both blind and sighted people.

The available data fail to distinguish unambiguously between modality-invariance and modality-flexibility in the case of objects for another reason. The neural dissociations of the categories represented in ventral temporal cortex could be described either in abstract or in sensory terms. Are objects represented in ventral temporal cortex because of the particular relevance of visual shape and colour information to categorizing objects during development? Alternatively, have humans evolved neural mechanisms within ventral temporal cortex for picking out the ontological category of physical objects? Are artifacts and animals neurally dissociable because of abstract distinctions? Even preschoolers know that whether something is a chair depends to a large degree on the intent of the agent that made it, whereas whether something is a cow depends on its biological origins (Greif, Kemler Nelson, Keil, & Gutierrez, 2006). Alternatively, are these categories neurally dissociable because of sensory differences in their shape and size? As we argue below, the neurobiological evidence for modality-invariance is clearer in the case of action concepts.

## Neural basis of action concepts in blind individuals

Actions make up another conceptual category that is believed to have a prominent visual component, especially from visual motion. People use patterns of visual motion to categorize events as "bouncing" versus "rolling", and to differentiate between "he jumped" versus "he was jumping" (Baldwin, Andersson, Saffran & Meyer, 2008; Baldwin et al., 2001; Zacks, Kumar, Abrams & Mehta, 2009). According to the modality-dependent hypothesis, action concepts are in part *comprised* of images of these visual motion patterns (Kable, Kan, Wilson, Thompson-Schill & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002; McClelland & Rogers, 2003; Pulvermuller, 1999). Apparently consistent with this prediction, multiple neuroimaging studies report that

listening to action-verbs engages posterior lateral temporal regions, in or near visual motion areas (Chao, Haxby, & Martin, 1999; Kable et al., 2002, 2005; Kemmerer, Castillo, Talavage, Patterson & Wiley, 2008; Martin, Haxby, Lalonde, Wiggs & Ungerleider, 1995; Revill, Aslin, Tanenhaus, & Bavelier, 2008; Tettamanti et al., 2005; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003).

If action concepts of sighted people are composed in part of visual motion images, then the action concepts of blind individuals should be substantially different from those of the sighted. We tested this hypothesis by asking a group of congenitally blind individuals to perform a semantic similarity task with action-verbs and object-nouns. Participants judged pairs of action verbs or object-nouns on how related in meaning they were (e.g., "to kick" and "to run"; "the bush" and "the tree"). Behaviourally, blind people performed the similarity judgements just like sighted participants. The ratings of blind people were just as highly correlated with the ratings of sighted people as were the ratings of two different groups of sighted individuals. Blind and sighted people's ratings were just as highly correlated for manner of motion verbs (e.g., to kick, to roll) as for abstract mental state verbs (e.g., to think) (Bedny, Pascual-Leone, & Saxe, 2009; Koster-Hale, Saxe & Bedny, 2012). At least with regard to these simple kinds of semantic judgements, blind people appeared to have intact semantic representations of actions, providing evidence against the modality-dependent hypothesis.

Still, these behavioural data leave open both the modality-flexible and modality-invariant hypotheses. Where sighted people rely on visual images to decide how similar rolling is to bouncing, blind people might retrieve images in other modalities that efficiently compensate for lack of vision. Since vision, touch, and motor control are supported by distinct parts of cortex, neuroimaging studies could distinguish between these hypotheses. For example, the modality-flexible hypothesis predicts that sighted people activate visual motion circuits during action verb comprehension, whereas blind individuals rely on the

motor and/or tactile system to a greater extent. By contrast, if blind and sighted people rely on similar neural circuits this would provide further evidence that these populations rely on similar cognitive mechanisms for understanding action verbs (modality-invariant hypothesis).

To test these hypotheses we scanned blind and sighted participants while they performed semantic similarity judgements with action verbs and object-nouns. As in Mahon's studies of object concepts, we found preserved neural responses to action-verbs (compared to object-nouns) in people who are blind. Like sighted people, congenitally blind individuals activated the left middle temporal gyrus (LMTG) when they made semantic decisions about action-verbs, but not when they made similar decisions about object-nouns (Bedny, Caramazza, Pascual-Leone & Saxe, 2012; Noppeney et al., 2003). The LMTG responses in blind people were similarly localized, of equal neuroanatomical extent, and equally robust. The presence of a typical LMTG response in people who have never seen makes it less likely that this brain region represents visual images of motion. More generally, there were no responses anywhere in the brain that were present in sighted people but missing in people who are blind, proving strong evidence against the modality-flexible hypothesis.

Importantly, we also found no evidence that blind individuals retrieved more motor or auditory−sensory information during action-verb comprehension, contrary to the predictions of the modality-flexible view.

Still, as in the case of objects, it is possible that the modality-flexible hypothesis is correct: Rather than relying on classic tactile and motor regions, blind people may have developed tactile and motor representations of motion in the same cortical location where sighted people represent visual motion, via crossmodal plasticity. For example, the LMTG might represent visual motion images of actions in sighted people, and tactile, auditory, or motor motion images of actions in people who are blind.

To test whether the representations of actions in LMTG are representations of motion patterns in any modality, we presented sighted and blind participants with noun and verb categories that varied in visual motion features. Visual motion brain regions that support seeing the movement of inanimate and animate objects all respond more to moving than to nonmoving visual stimuli (de Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994; Tootell et al., 1995a). If the LMTG stores perceptual motion information, it should also respond more to actions with than without motion.

Participants heard low-motion verbs (e.g., "to think"), medium-motion verbs (e.g., "to bleed"), and high-motion verbs (e.g., "to kick") as well as low-motion nouns (e.g., "the rock"), medium-motion nouns (e.g., "the broom"), and high-motion nouns (e.g., "the tiger"). Surprisingly, we found that the LMTG response is invariant with respect to motion information. The LMTG responds more to all verbs than to all nouns, irrespective of motion features. For example, the LMTG response was equally high for low-motion verbs such as "to think" and high-motion verbs such as "to kick." The LMTG response was equally low for high-motion nouns (e.g., "the tiger") and low-motion nouns (e.g., "the rock") (for converging evidence see Grossman et al., 2002; Rodriguez-Ferreiro, Gennari, Davies, & Cuetos, 2011). If anything the response of the LMTG was slightly higher for mental state verbs than action verbs. Furthermore, this response profile of the LMTG was identical in sighted and blind individuals across seven word categories. Finally, while we found robust effects of grammatical class on neural responses, we found no brain regions that responded more to high-motion verbs than to low-motion verbs (Figure 2, left panel).

These findings provide several different kinds of evidence for modality-invariant and abstract representations of actions. First, the LMTG, which was hypothesized to store visual images of motion, does not store visual information, does not store motion information and does not depend on early visual experience for normal development. In general, we find no evidence that visual motion associations predict neural responses to words anywhere in the brain. Nor is there any evidence that the neur'obiology of
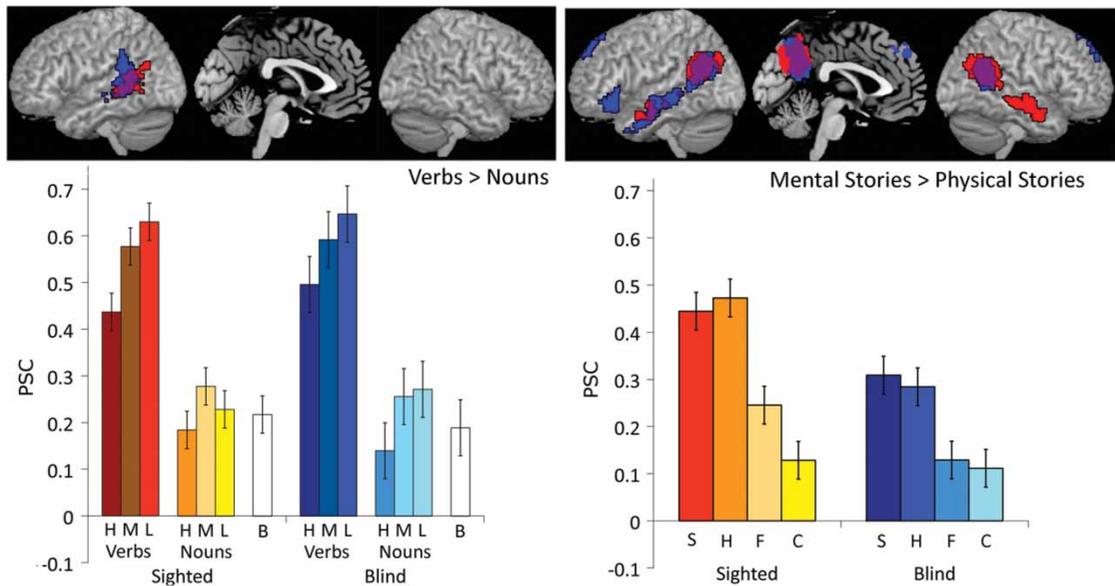
**Figure 2.** *Neural activity during verb and noun comprehension (left) as well as mentalizing (right) in blind and sighted individuals. Top left panel shows results of whole-brain random effects analyses for sighted (red) and blind (blue) groups, corrected for multiple comparisons, p < .05. On the left are greater responses to verbs than nouns. Bottom left bar chart shows percent signal change (PSC) in the left middle temporal gyrus for verbs and nouns with varying degrees of visual motion information. Bars for higher motion words are displayed in darker colours: high motion (H), medium motion (M) low motion (L), backwards speech (B). Regions of interest were defined in individual subjects based on the verb > noun contrast (Bedny et al., 2011c). Top right panel shows neural response to stories about mental states as compared to stories about physical events. Right bar chart shows percent signal change in right temporoparietal junction for stories about mental states based on seeing (S), mental states based on hearing (H), bodily feelings, e.g., hunger (F), and control stories about physical events (C). To view a colour version of this figure, please see the online issue of the Journal.*

action concepts is different in congenitally blind individuals as compared to sighted people. By contrast, neural responses are sensitive to abstract features of words that are not reducible to perceptual primitives: namely their grammatical class (Hillis, Wityk, Barker & Caramazza, 2003; Shapiro & Caramazza, 2003; Yokoyama et al., 2006).

What exactly does LMTG represent about verbs? Based on our data, the LMTG could store abstract conceptual information relevant to verb meanings or grammatical information associated with verbs (Bedny et al., 2011a). Some evidence favours a role for the LMTG response in conceptual, rather than grammatical, processing. Several studies have reported LMTG responses to familiar actions in nonverbal tasks (Galati et al., 2008; Ricciardi et al., 2009) and damage to the LMTG impairs people's ability to match verbs to

appropriate action videos (Kalenine, Buxbaum, & Coslett, 2010). In a recent experiment, we found that part of the LMTG responds not only to verbs, but also to event nouns (e.g., "the wedding") (Bedny, Dravida, & Saxe, 2012; see also Bedny & Thompson-Schill, 2006). Such findings suggest that the LMTG may store information relevant to lexicalized event categories (Frawley, 1992). Future studies of languages with distinct conceptual to linguistic mappings could yield important insights into the nature and developmental origins of the LMTG responses to verbs (e.g., De Bleser, 2003). Whatever the precise nature of LMTG representations, they are deployed during word comprehension and they develop independent of visual experience.

These findings suggest that action concepts retrieved during word comprehension and simple

semantic judgements are modality-invariant. An interesting question concerns what kinds of tasks and stimuli engage these modality-invariant representations. There is some evidence that modality-invariant action representations are retrieved based on nonverbal materials. Congenitally blind individuals activate similar neural circuits to sighted people when they listen to action sounds (e.g., knocking or clapping) and remember action sequences. In both populations these kinds of tasks recruit not only lateral-temporal areas, such as the LMTG, but also left-lateralized areas in parietal and prefrontal cortex (Alaerts, Swinnen & Wenderoth, 2011; Fiehler, Burke, Bien, Roder, & Rosler, 2009; Lewis et al., 2011; Ricciardi et al., 2009).

In sum, blind and sighted people talk about actions and objects in similar ways and make similar semantic judgements about action and object categories. Drastic changes in sensory experience do not have equally drastic consequences for what people know about objects and actions (contrary to the modality-dependent hypothesis). Neuroscientific studies further suggest that similar behaviour of blind and sighted people is not masking qualitatively different formats of knowledge (contrary to the modality-flexible hypothesis). People who have never seen, and thus could not have learned concepts through vision, rely on neurobiologically similar representations of actions and objects. The same changes in sensory experience that reorganize the visual system have little, if any, consequence for the neurobiology of concepts. We hypothesize that these conceptual systems would show plasticity, and experience-dependence, in cases of qualitative change to the abstract experience relevant to those systems. Growing up isolated from objects or actions might lead to qualitatively different concepts. Finally, sensory dimensions that describe the neurobiological organization of the visual system (e.g., presence of motion) do not describe the organization of conceptual systems in either sighted or blind people. Instead, the neurobiology of concepts is organized along abstract dimensions (e.g., events versus entities). Humans possess modality-invariant and abstract conceptual representations of objects and actions, which are equally accessible to sighted and blind people.

## Concepts of mental states: Behavioural and neuroscientific studies of Theory of Mind in blind individuals

The role of sensory experiences in conceptual development has also been hotly debated in a second domain: explicit thinking about other minds, or "Theory of Mind" (ToM). When we think about other people, we are often most interested in the abstract, invisible contents of their minds: their thoughts, motivations, hopes, dreams, and fears. Yet our own sensory experiences might be a gateway to understanding other minds: First, sensory experience gives us access to other people, allowing us to witness their actions and reactions; and second, our own sensory experience gives us a model for what it's like to have a mind, or experiences, that is "like me" (Meltzoff, 2005, 2007). For example, we might understand what it's like to learn through seeing because we ourselves can see. Since both of these sources of evidence are diminished for congenitally blind children, blind people might have very different concepts of other people's minds as compared to sighted people.

Development of ToM could depend on vision in at least two quite different (but not mutually exclusive) ways. First, vision is the dominant modality by which human infants learn about distal events, until they can use language. Other people's goal-directed actions, and attention, are frequently deployed in ways that are accessible by vision but not by other senses. For example, someone across the room might reach for a teddy bear, grab it, and smile, signalling successful completion of a goal-directed action; this whole sequence would be inaccessible for a blind child. There is extensive evidence that young sighted infants pay close attention to others' actions and facial expressions, and form rich expectations about how those actions will unfold. For example, sighted infants expect that people will reach for objects that they previously looked at

(Luo & Johnson, 2008), and that people's actions are oriented towards objects rather than places in space (Woodward, 1998). By age 10 months, infants also actively coordinate their direction of visual attention with an adult, using both gaze direction and (later) pointing to establish joint attention for communication. By age two years, infants expect an actor to reach for an object in the place where the actor last *saw* the object, showing that they track others' visual histories as well as current visual access (Baillargeon, Scott, & He, 2010; Luo & Baillargeon, 2007; Southgate, Senju, & Csibra, 2007). All of these early experiences with human actions feed into later conceptual developments; infants' visual expectations regarding goal-directed action at nine months predict their conceptual understanding of other people's beliefs three years later (Wellman, Lopez-Duran, LaBounty, & Hamilton, 2008).

Absence of visual access to others' actions is one limitation for blind children; another is the absence of visual experience itself. Given that other people's internal experiences are always inaccessible, one way children might learn about other minds is by assuming that other minds are similar to their own. That is, to figure out what an actor is experiencing, the observer could think: "What *would I* be experiencing, if I were in the actor's position?" This idea, known as the "like me hypothesis" (Meltzoff, 2007) or (relatedly) simulation theory, suggests that we understand others by assuming that they are similar to ourselves (Gallese, 2007). For example, preverbal sighted infants expect that other people's visual experiences are similar to their own; thus, after wearing an opaque blindfold and experiencing the absence of vision (but not before this experience), sighted infants expect that an adult wearing the same blindfold cannot see (Meltzoff & Brooks, 2008). If similar experiences are a necessary bridge for "simulating" other people's minds, then blind children would again be stymied, since the sighted people around them have many experiences that are fundamentally dissimilar from their own.

All of these reasons suggest that people who grow up blind might have a different

understanding of other minds than sighted people do. By contrast, in explicit conversation and experiments, congenitally blind adults appear to have a very rich understanding of minds in general, and experiences of sight in particular. Landau and Gleitman (1985) asked a congenitally blind woman to define a range of verbs of seeing. Her definitions suggest a deep and subtle appreciation of the experience of sight. For example, she defined *to dazzle* as "to brighten, make it so bright that you can't see for a second, something sudden, like turning on a bright light in a dark room." We recently asked a group of congenitally blind adults to make semantic similarity judgements on verbs of perception (e.g., to spot, to peek) and visual quality (e.g., to sparkle, to flash). Remarkably, the judgements of congenitally blind individuals were highly similar to those of sighted people—just as similar as those of sighted people to each other. Judgements of congenitally blind individuals were also equally similar for visual verbs and for auditory (to boom, to crackle) and tactile verbs (to touch, to feel). Cluster analyses show that blind people distinguish verbs of visual perception from verbs of touch and verbs that are not tied to a particular modality (e.g., to investigate). In an experiment with narratives, we found that blind adults performed exactly as well as sighted adults on simple tests of understanding other minds (e.g., tracking what others believe, and predicting their emotions; Bedny et al., 2009).

These data raise the same challenge that we described above, for conceptual representations of actions and objects. If a blind adult can appropriately use words for, and answer questions about, mental states including visual experiences, does that mean that blind adults have the same concepts of beliefs, thoughts, and perceptions as sighted people? Or are verbal behaviours covering up fundamental differences in the ways that sighted and blind people think about the mind? As above, functional neuroimaging provides a complementary source of evidence to behavioural judgements. We can look "under the hood", and ask whether the neural circuits activated for thinking about the mind, in general, and experiences of seeing,

in particular, are similar or different in sighted and blind adults.

We conducted a neuroimaging experiment to test these hypotheses. First, we asked sighted and blind adults to listen to stories about people's thoughts and beliefs, versus stories about other physical representations, such as maps, photographs, and audio recordings. Dozens of prior neuroimaging studies (Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005) had found that reading about people's thoughts leads to increased activity in a group of brain regions, including bilateral temporo-parietal junction (TPJ), medial prefrontal cortex (MPFC), and medial parietal cortex (precuneus, PC). Of these regions, the TPJ was specifically thought to depend on visual input. The TPJ is adjacent to brain regions recruited during visual observation of human bodies and actions (Downing, Jiang, Shuman, & Kanwisher, 2001; Grossman & Blake, 2002), and when considering others' gaze direction and visual perspectives (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Pelphrey, Morris & McCarthy, 2004; Wyk, Hudac, Carter, Sobel & Pelphrey, 2009). Thus, it seemed plausible that the development of the TPJ might depend on visual input from its neuroanatomical neighbors during childhood. Contrary to this hypothesis, we found that all of the so-called "ToM regions" appeared identical in size and position in sighted and congenitally blind adults (Bedny et al., 2009). Thus, visual access to others' actions and gaze direction does not seem to be necessary for typical development of ToM brain regions (Figure 2, right panel).

Converging evidence for the same conclusion comes from Ma and colleagues (Ma & Han, 2011). Blind and sighted adults were asked to attribute traits to themselves and others (e.g., "lazy", "courageous"). Both blind adults (listening to trait words) and sighted adults (reading trait words) showed enhanced MPFC activity when attributing traits to themselves. Also, blind adults are actually better than sighted adults at recognizing emotional tone of voice and have increased neural markers of emotional response to voices (Klinge, Roder, & Buchel, 2010). Taken together,

these three studies suggest that visual access is not necessary to develop typical "social" brain regions.

Second, we (Bedny et al., 2009) tested the "simulation" hypothesis that we understand other people's sensory and mental experiences by, in a sense, feeling what it would be like to have that experience in our own mind. Blind people have some of the same mental experiences as sighted people (e.g., hearing the sound of a baby laughing, hearing a friend's footsteps) but do not have other experiences (e.g., seeing a baby smiling, seeing a friend's handwriting). If blind and sighted people actually have fundamentally different representations of experiences of seeing, in spite of their similar language use, then we should see those differences in patterns of neural activation. By contrast, we again observed that blind adults' neural responses looked just like sighted adults'. Both blind and sighted adults showed robust activity in "ToM" brain regions when listening to stories about hearing and about seeing; there was no region anywhere in the brain that showed different responses to hearing versus seeing, in blind versus sighted people (Figure 2, right panel). These data could suggest that blind people treat seeing and hearing experiences as equivalent. That is, perhaps blind people interpret "to see" as "to perceive". Contrary to this interpretation we found that we could distinguish stories about seeing from stories about hearing based on the pattern of neural activity within the RTPJ (Koster-Hale, Bedny, & Saxe, 2012). Together, behavioural and neuroimaging data suggest that blind people have rich representations of seeing, despite never having seen.

Neuroimaging studies with blind adults thus provide evidence for preserved understanding of other minds despite differences in first person sensory experience. Apparently, by adulthood, understanding "running" does not necessarily involve a visual image of running, understanding "wanting" does not require watching someone reaching for an object, and even understanding "seeing" does not require first-person experiences of vision.

Interestingly, though, the developmental processes by which blind and sighted children arrive

at an adult ToM may be different. Although blind adults appear to have unaffected ToM (at least on simple tasks), blind children are delayed in developing an understanding of visual perception (Bigelow, 1991, 1992; Millar, 1976). For example, the blind six-year-old, Kelli, understood that sighted people can see with their eyes. But she also claimed that if a sighted person closed their eyes, they could see through their mouth, provided there was no food in it (Landau & Gleitman, 1985). Blind children are also worse than age-matched sighted children at reasoning about line of sight and partial occlusion of one object by another (Bigelow, 1991, 1992; Millar, 1976). Delays in understanding visual experience may reflect the absence of first-person experience, and the analogy from other minds to my own experience (the "like me" hypothesis; Meltzoff, 2007).

More generally, blind children also show delays on standard milestones of ToM development, such as false-belief tasks, which tap children's understanding that other people can have incorrect beliefs about the state of the world, caused by misleading, incomplete or outdated evidence. Blind children are late to pass classic false-belief tasks, even those that do not require an understanding of visual perspective (McAlpine & Moore, 1995; Minter, Hobson, & Martin, 1998); and blind children continue to fail false-belief tasks after they catch up with sighted children on visual perspective-taking tasks (Peterson et al., 2000). Delays on false-belief tasks generalize across paradigms (e.g., the Sally Anne task) (Brambring & Asbrock, 2010; Green, Pring, & Swettenham, 2004; Peterson et al., 2000), and persist even when blind children reason about the mental states of other blind children (Peterson et al., 2000) and when tasks do not require visual knowledge of objects (Brambring & Asbrock). For example, in one auditory false-belief task, an experimenter played a familiar song to blind children. The song was stopped in the middle and the children were asked what they expected to hear when the player was turned on again. The children then heard an unexpected continuation of the song (e.g., the wrong phrase). Afterwards, children were asked: When I play the beginning of this song to your friend, what will *she* expect to hear? "Passing" the false-belief task requires children to predict that another child will expect to hear the correct continuation. Whereas almost all sighted children pass this task by five years of age, blind children do so by six years of age. On average, across 16 different ToM tasks specifically designed for blind children, blind children are delayed by 19 months relative to blindfolded sighted control children (Brambring & Asbrock, 2010).

Thus, losing visual access to other people does seem to delay development of children's ToM. One very interesting open question is *when* the delay occurs. Are blind infants delayed in developing initial nonverbal (perhaps implicit) expectations about others' actions, which then translate into later development of explicit conceptual understanding of mental states (Wellman et al., 2008)? Or do blind children show typical early stages of "theory of mind", including understanding of goals and desires, but then make a slower transition to a fully representational conception of beliefs? Future research with young blind children, and mental concepts beyond seeing and believing, is necessary to resolve this question.

Functional neuroimaging could be used to further investigate the origins of ToM deficits in blind children. Performing a false-belief task depends on many different cognitive abilities, including ToM, but also language and executive function (i.e., the ability to hold in mind and choose between multiple competing ideas (Flynn, O'Malley, & Wood, 2004; Rakoczy, 2009). Each of these cognitive capacities is associated with activity in different groups of neural regions (Botvinick, Cohen, & Carter, 2004; Friederici, 2002; Grodzinsky & Friederici, 2006; Miller & Cohen, 2001; Poeppel & Hickok, 2004; Price, 2000; Thompson-Schill, Bedny, & Goldberg, 2005). Thus, neuroimaging would allow us to test whether delays in ToM task performance in blind children are related to delayed development of domain-specific brain regions for ToM, or rather to differential development of the many other cognitive functions required for passing ToM tasks.

It may also be illuminating to compare the effects on ToM development of blindness versus deafness. Whereas blindness leads to a brief but significant delay in basic ToM milestones, deaf children show no delay in passing false-belief tasks, unless they are born to nonsigning parents. Absence of early *auditory* access to the world, *per se*, does not impair ToM; and the presence of early auditory access does not seem sufficient to support typical ToM development. These results converge to highlight the importance of early visual access to other people, at the first stages of ToM development.

On the other hand, early language deprivation can have longer lasting and more profound consequences for the development of ToM than blindness. Deaf children of non-native-signing parents can be delayed two to three years on standard ToM milestones (Peterson & Siegal, 1995; Pyers, 2006; Schick, de Villiers, de Villiers, & Hoffmeister, 2007; Woolfe, Want, & Siegal, 2002), and their performance, even on low-verbal versions of ToM tasks, is predicted by their parents' use of mental state verbs in sign language (Moeller & Schick, 2006). Strikingly, exposure to people talking about the mind appears to be a necessary gateway to a full ToM. Adults whose language does not contain mental state terms fail basic nonverbal false-belief tasks (Pyers & Senghas, 2009). When the content of the language changes, to include mental state terms, these adults show corresponding improvements on false belief tasks (Pyers & Senghas, 2009). It seems that visual access to other people cannot compensate for the evidence provided by language and conversation. By contrast, linguistic access can compensate for vision. Between age seven years and adolescence, blind children catch up with their sighted peers in performance on theory of mind tasks (Brambring & Asbrock, 2010).

Based on the developmental evidence, we hypothesize that learning about other minds proceeds in two phases. Prelinguistic infants learn about the minds of others primarily through visual access to human faces, eyes, and actions and through their own first-person experiences of seeing. With increased linguistic abilities, children rely heavily on language and in particular on learning from other people talking about the mind. As a result, lack of vision leads to slow initial development of social knowledge, but the resulting delays are eventually overcome by blind children—at least in part through evidence from language (see Urwin, 1983 for related ideas).

In sum, neuroimaging provides a new window into blind people's understanding of other minds. Corroborating behavioural evidence, neuroimaging results suggest that blind adults acquire complete and typical representations of other people's mental experiences, even experiences of seeing. On the other hand, blind children's development of mental state representations is slow. This slowing is not particular to representations of seeing, but likely results from reduced access to visual evidence of mental states. In the future, neuroimaging may facilitate discovering the cognitive origin of this delay.

## Objects, actions, and thoughts in the minds of blind people: Some qualifications

Studies of blindness thus place an upper bound on the strength of the link between percepts and concepts. While the sensory experience of blind and sighted people is drastically different, behavioural and neuroimaging data show that conceptual representations of these two groups are strikingly similar. These similarities hold for conceptual categories that, in our view, are among the best candidates to show effects of blindness. Conceptual representations used to understand concrete words, categorize objects and actions, and think about the perceptual states of other people are not images of sensory experiences. Humans have a rich repertoire of abstract representations that capture the higher-order structure of their environment in terms of events, objects, agents, and their mental states. In this regard, neuroscience affirms rather than undercuts a basic tenet of modern cognitive science, that abstract representations are just as real in the mind and brain as representations of shape, colour, and orientation (Bedny & Caramazza, 2011; Caramazza & Mahon, 2003; Chatterjee, 2010;

Dove, 2009; Mahon & Caramazza, 2008; Potter & Faulconer, 1975; Potter, Valian, & Faulconer, 1977).

One question raised by this argument, however, is: Where is the boundary of a concept? In our experiments, and our review above, we have focused on abstract aspects of concepts that are necessary for understanding words and making simple inferences. In addition to this putative core, concepts are associated with lots of other information, including sensory images. In many conceptual tasks, sighted people can and do retrieve such visual knowledge (Thompson-Schill, 2003; Wilson, 2002). For example, visual information is used to make detailed judgements about the appearance of objects, such as their colours, shapes, and sizes (e.g., does a kangaroo have a long or short tail?) (Farah, Hammond, Levine, & Calvanio, 1988; Hsu et al., in press) and to answer questions about spatial layouts (e.g., how many windows are there in your kitchen?). We believe that the studies done to date have not tested blind individuals on tasks that are likely to depend on visual information in sighted individuals.

How do these phenomena relate to claims about amodal concepts? We expect that blind people *would* show differences from sighted people in how they performed image-based tasks, like counting their kitchen windows or deciding whether a stop sign is darker than a carrot. These differences would be manifest in their behaviour or neural responses or, more likely, both (Arditi, Holtzman, & Kosslyn, 1988). One interpretation is that amodal conceptual representations are distinct from sensory images, but both kinds of representations exist and can dynamically interact to support task performance. Similar interactions occur between different sensory systems. For example, auditory information affects both visual perception and processing in early visual areas of the human brain (Sadaghiani, Maier & Noppeney, 2009). A natural interpretation is that auditory and visual representations are distinct, but can interact and influence one another. In a similar way, sensory representations might contribute to conceptual tasks (Mandler, 2008).

Another possibility is that there is no clear distinction between conceptual and sensory representations; there is just a continuum of different kinds of knowledge. On this view, the data we have described show that blind and sighted people share one aspect of object and event concepts (the abstract features retrieved when understanding words and sentences), but other aspects of those same concepts (the sensory images used to make judgements about appearance) might be different. Data from blind individuals would then inform hypotheses about when these different aspects of knowledge are deployed: Whenever blind and sighted people show similar performance and similar brain activation, only the abstract features of conceptual knowledge are necessary for task performance.

These reflections also relate to another issue. Here we argue that blind and sighted people have roughly similar concepts of objects, actions, and sight, but the experiments to date have barely scratched the surface of these representations. When we probe in more detail, blind and sighted people will likely differ not only in the sensory images associated with their abstract knowledge, but in the fine-grained details of the abstract knowledge itself. Such differences might be analogous to differences between experts and non-experts in other cognitive domains (e.g., mechanics, marine biologists, and wine tasters) (Ballester, Patris, Symoneaux & Valentin, 2007; Goldberg & Thompson-Schill, 2009). The difference between a layman's and a marine biologist's representation of lobsters is not just that the former is gustatory while the latter's is visual. A marine biologist has significantly more detailed knowledge about lobsters: how they breathe, how they eat, and what their nervous system is like. Similarly a blind person might be less likely, on average, to know whether a hippopotamus has fur, and more likely to know about the cognitive capacities of guide dogs, the social networks of the blind community, and people's perception through touch. It may be particularly interesting to ask whether blind individuals differ in their fine-grained knowledge of sight (Heller & Kennedy, 1990). Do blind individuals have less

detailed knowledge of occlusion, visual attention, line of sight, etc.? Neurally, such knowledge differences between blind and sighted people would likely be reflected in the information coded within similar brain regions, rather than in which brain regions store conceptual representations. Such conceptual differences across populations could be characterized by measuring behaviour and examining neural responses at higher spatial resolution, for example with multivoxel pattern analysis and fMRI adaptation (Druks & Froud, 2002; Pietrini et al., 2004). We hypothesize that conceptual differences between blind and sighted people are quantitative rather than qualitative. These differences, if they exist, are similar in kind to conceptual differences caused by other naturally occurring variation in life experiences, such as variation across cultures and professions. Just as we would say that the biologist and the layman share qualitatively similar concepts of lobsters, blind and sighted people share qualitatively similar concepts of objects, actions, and mental states.

## CONCLUSIONS

Blindness has long been a window into the origins of the human mind, but often as a thought experiment. During the past century, cognitive scientists have tackled old philosophical puzzles by applying the methods of experimental psychology and neuroscience to the study of blindness. Rather than postulate what the minds of blind people should be like, cognitive scientists have collaborated with blind individuals to test theories of development. This effort has yielded a rich set of data that constrains cognitive and neuroscientific theories of development.

Studies of blindness reveal that brain regions with strong innate biases have a dramatic capacity for change. In children who grow up without sight, visual circuits develop drastically different cognitive functions. Contrary to what most theories of neurobiological development would predict, this neuroplasticity does not respect cognitive boundaries. The same brain regions that

support visuospatial discrimination in sighted people participate in abstract cognitive functions, such as language, in blind individuals. Visual cortex plasticity demonstrates the pluripotency of human neural circuits during development.

While developmental blindness profoundly reorganizes brain regions that encode the surface structure of the visual world, it leaves the neurobiology of concepts largely unchanged. This neuroscientific observation augments behavioural evidence of preserved conceptual knowledge in people who are blind. Even in the case of concrete categories of objects and actions, blind people know similar information and this information is implemented in similar neural systems. Contrary to the suppositions of the empiricist philosophers, blindness does not qualitatively change the nature of concepts. In blind and sighted people alike, seemingly concrete concepts have core abstract components that develop independent from the sensory quality of experience.

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