

# Convergence and divergence in a neural architecture for recognition and memory

Kaspar Meyer and Antonio Damasio

Brain and Creativity Institute, University of Southern California, 3641 Watt Way, Los Angeles, CA 90089-2520, USA

**How does the brain represent external reality so that it can be perceived in the form of mental images? How are the representations stored in memory so that an approximation of their original content can be re-experienced during recall? A framework introduced in the late 1980s proposed that mental images arise from neural activity in early sensory cortices both during perception and recall. Neurons in the association cortices, by contrast, would not code explicit mental content; rather, they would hold the records needed to reconstruct an approximation of the original perceptual maps in early cortices. Several neurophysiological and neuroimaging studies now lend growing support to this proposal.**

A remarkable activity of the human brain consists of creating mapped representations of reality in its sensory cortices, such as visual, auditory or somatosensory, and permitting the experience of those maps in the form of mental images. A no less remarkable activity consists of creating memory records of the sensory maps and playing back an approximation of their original content during recall. How does the brain establish the record of a map, and where is that record located? Just as importantly, where is the record played back during recall, such that the essential properties of the original image can be re-experienced?

A widely accepted answer to these questions is inspired by the traditional account of sensory perception. Accordingly, the components of perceptual information provided by varied early sensory cortices are projected forward to multimodal association cortices in a stepwise manner. This processing cascade is assumed to culminate in the anterior parts of the frontal and temporal lobes, where integrated mental images of ongoing reality would be generated. This account is exemplified by the notion of ‘grandmother cell’, a neuron (or small ensemble of neurons) at the top of the processing cascade whose activity would, all by itself, comprehensively represent our grandmother when we see her. Importantly, such neurons would not only fully represent objects and events during perception; once reactivated, they would also enable, again by themselves, recall of the same objects and events in their entirety, there and then.

In the logic of this view, lesions in the anterior temporal and frontal cortices should preclude both normal perception and normal recall. However, this prediction is not

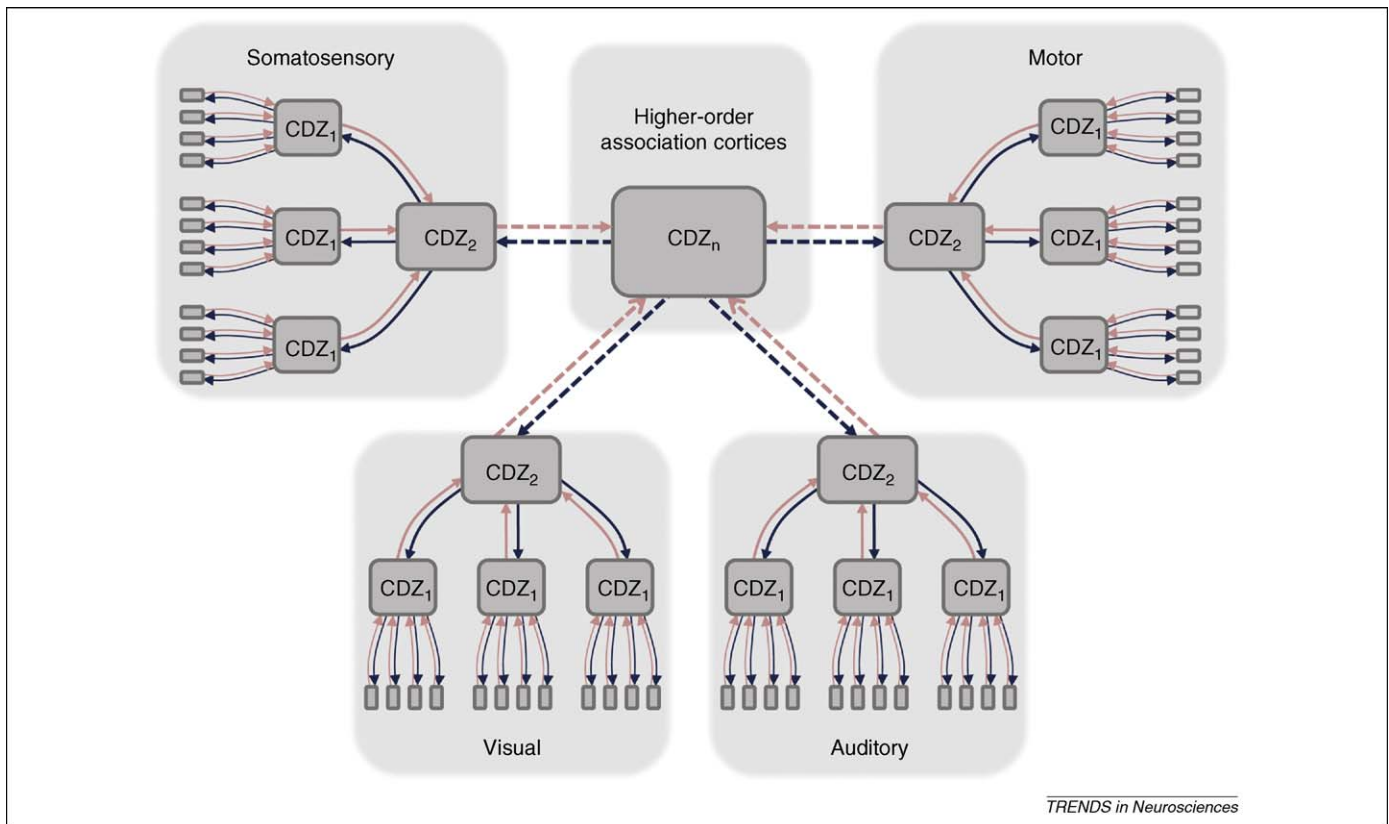
borne out by neuropsychological findings. Patients with such lesions report normal perception and only display selective deficits in the recognition and recall of unique objects and events [1]. For example, the patients might describe in minute detail the contents of a picture presented to them, determine correctly that the picture displays a birthday party, and yet not recognize that it was in fact their own. In other words, damage to the cortices at the top of the processing cascade precludes neither integrated sensory perception nor retrieval of mental representations of objects or events at generic level (‘a birthday party’). However, it does preclude the recall of unique objects or events (‘the birthday party when I turned forty’).

Almost two decades ago, prompted by these observations, A.D. proposed a novel model of neural architecture aimed at accounting for recognition and recall [1]. The model was well received and has been adopted as a basis for comprehensive conceptualizations of cognition (see, for example, the work of Barsalou [2,3]). However, the early application of the idea was limited by the lack of empirical studies providing direct evidence for the proposed mechanism. Here, we review several electrophysiological and neuroimaging studies in the areas of sensory perception, mental imagery and mirror-neuron research that lend growing support to the proposal.

## The convergence-divergence-zone framework

The neural architecture proposed by A.D. is presented in detail elsewhere [1]; in this review, we can only provide a summary. The architecture is constituted by two crucial elements: (i) neuron ensembles in early sensory and motor cortices, which represent separate knowledge fragments about a given object; and (ii) neuron ensembles located downstream from the former in association cortices, which operate as convergence-divergence zones (CDZs; [Figure 1](#)). CDZs receive convergent projections from the early sensorimotor sites and send back divergent projections to the same sites. CDZs contain records of the combinatorial arrangement of the knowledge fragments coded in the early cortices, that is, they hold information about how those fragments must be combined to represent an object comprehensively. CDZ records are shaped by experience. When the organum interacts with an object, several aspects of the interaction are mapped simultaneously at separate sites in early sensorimotor cortices. The temporally coincident activity at the separate sites

Corresponding author: Meyer, K. ([kaspar.meyer@usc.edu](mailto:kaspar.meyer@usc.edu)).



**Figure 1.** Schematic of the CDZ framework. Neuron ensembles in early sensorimotor cortices of different modalities (represented by small rectangles) send converging forward projections (red arrows) to first-order CDZs (CDZ<sub>1</sub>s), which, in turn, project back divergently (blue arrows) to the early cortical sites. Similar convergent-divergent connectivity patterns interlink CDZ<sub>1</sub>s with CDZ<sub>2</sub>s and CDZ<sub>2</sub>s with CDZ<sub>n</sub>s in higher-order association cortices (via several steps not represented here; dashed arrows).

modifies the connectivity patterns to, from and within a shared CDZ downstream, with the result that the various fragments of information about the object become associated. The convergent–divergent connectivity principle exists at all levels of the processing hierarchy: just as first-order CDZs inscribe records of the combinatorial arrangement of knowledge fragments in early cortices, second-order CDZs inscribe records of the combinatorial arrangement of first-order CDZs, and so forth (Figure 1).

A crucial difference between the traditional account for sensory perception and that in the CDZ framework is that, in the latter, knowledge is not ‘transferred’ from early to higher-order cortical areas. The various knowledge fragments held in early sensorimotor cortices do not move up a processing hierarchy and do not have to be projected to a single anatomical site to enable the apprehension of an integrated, multimodal image. Neuron ensembles in higher-order cortices (i.e. CDZs) do not hold a processed version or a composite of the representations contained in lower-order cortices. Rather, CDZs register linkages among knowledge fragments; they contain a record of the combinatorial arrangement of the multi-site activities that describe an object during perception. Recall (or recognition based on a part of the original pattern) is achieved by means of retro-activation, when CDZs reinstate an approximation of the original multi-site pattern using divergent back projections. Thus, the CDZ framework posits that both during perception and retrieval from memory, the mental images we experience arise from activity in early sensorimotor sites. Neurons in association

cortices coordinate this activity but do not themselves provide the correlate of mental images. (We note that throughout this article the terms ‘mental image’, or simply ‘image’, do not necessarily denote conscious mental images. We believe that not all maps constructed in early sensory cortices become conscious mental images. In other words, maps in early sensory cortices would be necessary but not sufficient for the experience of conscious mental images.)

As the complexity of objects and events increases, the assembly of knowledge fragments required for their comprehensive representation also becomes more complex. Presumably, assembling the large number of individual knowledge fragments that unambiguously define a unique object or event (the birthday party held when one turned forty) would require the activity of CDZs at the highest levels of the processing hierarchy of the brain. Damage to cortical areas containing such high-order CDZs (i.e. to anterior sectors of the temporal and frontal lobes) would impair recognition and recall of unique objects and events. However, such lesions would leave unaffected integrated perception and recall at non-unique levels because early sensorimotor cortices and lower-order CDZs would be left unscathed. Thus, the CDZ framework can explain the dissociation of object recognition and recall between unique and generic levels observed in certain lesion patients.

Further support for the proposed brain architecture came from studies in experimental neuroanatomy that provided evidence for reciprocal signaling pathways between lower- and higher-order visual cortices [4] and be-

### Box 1. Backward projections reconstruct, rather than modulate

Reciprocal signaling in sensory systems has been firmly established and seems to be ubiquitous. Most cognitive neuroscientists have abandoned the idea of a purely unidirectional processing cascade in sensory processing pathways. Backward projections are traditionally thought to underlie feedback modulation ('top-down modulation'): activity in early cortices is influenced by factors such as attention, expectation and emotion, as well as by signals from the motor system (the latter enable stable percepts even though the body moves) [41].

In addition to top-down modulation, we propose another and very different role for backward projections: reconstruction of maps. Retro-activation does not simply modify bottom-up information that is already present in the early sensory cortices; rather, it uses information available in the association cortices and makes this information explicit by reconstructing maps in the early cortices.

Retro-activation is not only at work during mental imagery, a process manifestly supported by top-down activation. Rather, backward signaling occurs incessantly during perception, when it permits the completion of maps resulting from bottom-up processing and the reconstruction of additional maps in early cortices not targeted by bottom-up signals. The retro-activated maps code various aspects of knowledge associated with the perceptual stimulus. It is the (more or less complete) reassembly of this knowledge base that permits recognition of the stimulus.

tween widespread regions of the association cortices and the entorhinal–hippocampal formation [5] (Box 1).

Several neurophysiological and neuroimaging studies now provide additional support for the CDZ framework.

#### Perceptual processing

Most of the stimuli that occur in our environment are processed by the brain in more than one sensory modality. When someone talks to us in person, we simultaneously hear the speaker's voice and see the speaker's lips move. According to the CDZ framework, as a certain lip movement repeatedly co-occurs with a specific sound, the respective neural representations of the two events in early visual and auditory cortices will become associated via a binding record in a shared CDZ. Were we to have access only to the visual event (e.g. when watching a specific lip movement in a muted video clip), the activity pattern induced in the early visual cortices would trigger the CDZ and the CDZ would retro-activate, in early auditory cortices, the representation of the sound that usually accompanied the lip movement (Figure 2), even though that sound is not part of the current sensory environment. This prediction has been confirmed experimentally: reading lips in the absence of any sound induces activity in both primary and association auditory cortices (Brodmann's areas 41, 42 and 22), and the evoked activity patterns overlap considerably with those elicited during the perception of spoken words [6]. According to the CDZ framework, the meaning of a lip movement includes the sound typically associated with it, and the auditory map of that sound, therefore, has become an integral part of the lip movement's neural representation.

Many other studies have demonstrated cross-modal activations among various sensory modalities. Simply reading words with auditory or olfactory meaning evokes activity in auditory and olfactory cortices, respectively [7,8]. Tactile stimuli can activate brain regions tradition-

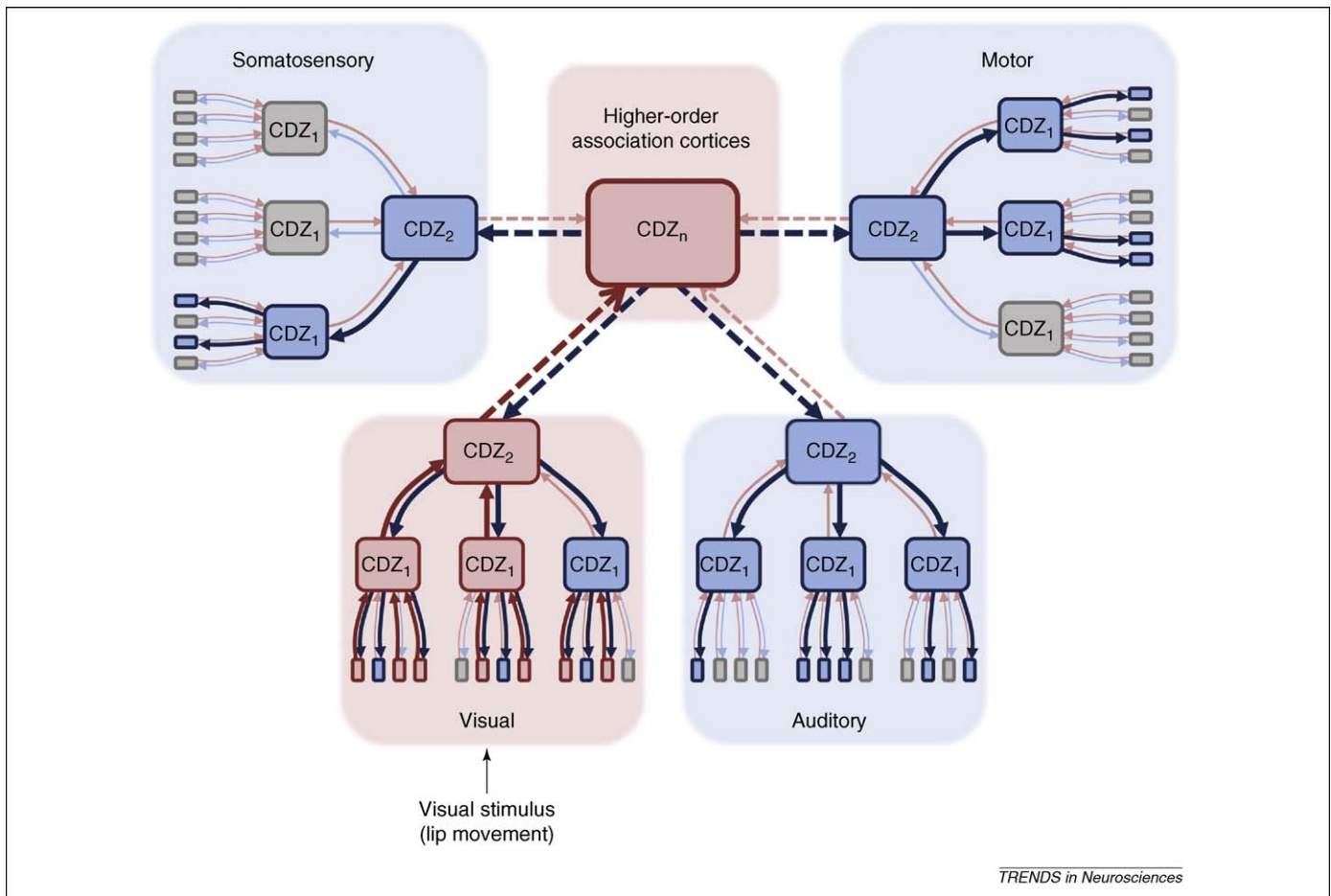
ally classified as unimodal visual areas in the absence of any visual percept. For example, when subjects feel brush strokes along their forearm and hand, activity can be observed in the middle temporal/V5 complex – a brain area traditionally believed to have a central role in the perception of visual motion – even when subjects have their eyes closed [9]. Furthermore, when subjects, again with eyes closed, use their fingers to discriminate the orientation of a tactile grid pattern, activity is observed in visual cortex, close to an area specifically recruited during visual discrimination of the orientation of grid patterns [10]. These cross-modal activations of the visual cortex are functional rather than spurious: subjects perform less well in the tactile orientation-discrimination task when the activity in the visual cortex is disrupted by transcranial magnetic stimulation (TMS) [11].

Cross-modal activations also have been demonstrated at the single-cell level. In a delayed visuo-haptic matching task [12,13], monkeys first saw a visual stimulus consisting of either horizontal or vertical black and white parallel stripes (cue period). Several seconds later, the animal had to touch two cylindrical bars that differed only in the orientation of ridges on their surface (horizontal versus vertical) and had to indicate which one of the bars corresponded to the visual stimulus it had seen before (choice period). In this task, after training, many cells recorded in the primary somatosensory cortices responded during the presentation of the visual cue, although the animal kept its hand on a rounded handrest during this interval. Of those cells that displayed stimulus selectivity during the choice period (i.e. differing firing rates when the animal touched the bar with horizontal or vertical ridges), a majority displayed coherent selectivity to the visual cues. In other words, a somatosensory neuron that fired more strongly when the animal touched the bar with the horizontal ridges would, in most cases, also react more strongly when the animal saw the horizontal visual cue. The authors concluded that 'by association, the visual cue may activate the internal representation of a tactile stimulus' [13], which is the core statement of the CDZ framework.

#### Mental imagery

There has been a long-standing debate regarding whether imagery occurs in a pictorial manner, conceived as a series of images (visual, auditory, etc.) [14] or relies on mental descriptions resembling those of language [15]. The CDZ framework provides a mechanism for the pictorial account, as it proposes that similar neural networks are activated when objects or events are processed in perceptual terms and when they are recalled from memory. The images constructed during perception should be re-constructed during imagery, not as perfect replicas and not necessarily as vividly, but as fainter approximations.

The work of Kosslyn [14,16–18] and others [19,20] indicates that imagery tasks in various modalities (e.g. visual, auditory and motor) usually evoke neural activation patterns that overlap considerably with those observed during perceptuomotor tasks in the same modalities. The networks activated during imagery include primary cortices, both for the visual [14,16–18] and the motor modalities [14,19]. Activation of primary visual



**Figure 2.** Convergent-divergent activation cascade upon seeing a lip movement. Visual apprehension of a lip movement elicits a specific activity pattern in early visual cortices (red rectangles). The two CDZ<sub>1</sub>s on the left (red) are activated by this activity pattern via convergent forward projections (bold red arrows); the CDZ<sub>1</sub> on the right is not. In this case, the specific activation pattern of CDZ<sub>1</sub>s activates the CDZ<sub>2</sub> and the CDZ<sub>n</sub> in higher-order association cortices (via several steps not represented here). The CDZ<sub>n</sub> sends divergent back projections (bold blue arrows) to CDZ<sub>2</sub>s in various sensorimotor areas (including the one in the visual sector that has promoted the forward activation cascade). Via further retro-activation of CDZ<sub>1</sub>s, the retro-activated CDZ<sub>2</sub>s reconstruct, in early cortical sectors, the activity patterns previously associated with the observed lip movement, for example the sound typically associated with it in addition to its motor or somatosensory representations (blue rectangles). Red designates areas activated by forward projections whereas blue denotes retro-activated areas. Note that the initial visual representation of the stimulus (both at the level of the CDZ<sub>1</sub>s and at the level of early cortical sectors) may be rendered more complete by means of retro-activation (parts of the visual sector colored in blue).

cortices during mental imagery seems to be topographical, just as during perception [16,17]. Also, disrupting primary visual cortex by TMS impaired performance in a visual imagery task [18], suggesting that activity in this area has a functional role in imagery. Furthermore, regions involved in processing specific visual stimuli, such as faces (fusiform face area) or places (parahippocampal place area), are also selectively activated during imagery of faces or places [20].

These findings dovetail with results from lesion studies that indicate that selective brain damage often causes parallel deficits in perception and imagery (e.g. an inability to both perceive and imagine colors) [14,21]. Evidence from both imaging and lesion studies thus suggests that memory recall of objects and events relies in part on neural activity at low levels of the processing hierarchy near sensory input and motor output sites and that the structures involved overlap considerably with those engaged in perceptual processing of objects and events.

The preceding section on perceptual processing provided evidence for the fact that perceiving unimodal stimuli can induce activity in early sensorimotor cortices

of other modalities. A comparable finding comes from so-called mental rotation tasks: behavioral data suggest that when subjects are asked to judge whether or not separate 3D objects, displayed at different spatial orientations, are identical, they proceed by mentally rotating one of the two objects to match it with the other [22]. Functional imaging indicates that motor cortices are activated during such tasks [23], presumably because subjects mentally rotate one of the objects with their hands. TMS of primary motor cortex disrupts performance in mental rotation tasks [24]. Once more, processing of a unimodal (visual) stimulus relies on representations held in cross-modal (motor) cortices; in this example, those representations do not describe what the visual object sounds or smells like but how it can be manipulated in motor terms.

### Mirror processing

Under normal circumstances, when we perform an action, we simultaneously apprehend what this action feels, looks and sounds like. In neural terms, an action does not merely consist of a sequence of movements coded by the motor cortices but also of several simultaneous sensory representations in somatosensory, visual and auditory cortices.

The CDZ framework suggests that the repeated co-occurrence of the various sensorimotor representations of a specific action leads to the establishment of convergent projections towards a common higher-order CDZ. As a consequence, when the same action is perceived, say, in visual terms, the activity pattern evoked in visual cortices triggers the CDZ, and the CDZ, through divergent back projections to early sensorimotor cortices, retro-activates representations of the action in other modalities (e.g. motor, somatosensory and auditory). We have recently proposed that cell ensembles in the classical mirror neuron (MN) areas of the brain (the caudal inferior frontal gyrus and the rostral inferior parietal lobule) operate as high-order CDZs for actions [25]. This view would provide a plausible theoretical account for the key finding of MN research: mere observation of actions leads to activity in MN areas [26,27].

Conceptualizing MNs as CDZs leads to additional predictions about brain activity patterns during action processing. First, action-related CDZs (i.e. MNs) should be activated by any of the sensorimotor activity patterns that represent a specific action (and not just by its visual description). Supporting this prediction, audio-visual MNs have been demonstrated in monkey brain area F5 [28,29]; these neurons are activated not only when the monkey performs or sees a specific action but also when it hears the consequences of the same action.

Second, according to the CDZ framework, MNs would not accomplish alone what is widely claimed to be their main function, namely, enabling the observer to grasp the meaning of an action. As noted, CDZs do not hold the meaning of objects and events themselves but, rather, establish meaning via time-locked multiregional retro-activation of early cortices. Accordingly, the meaning of an action (i.e. its more or less comprehensive sensorimotor description) could not be held by MNs alone but would depend on the reinstatement of various representations previously associated with the action and coded in several separate sites of early sensorimotor cortices. Several recent studies conducted in both monkeys and humans suggest that neural activity during action observation is indeed not limited to the classical MN regions but encompasses larger areas of premotor cortex [30–34], primary motor cortex [30,31], primary and association somatosensory cortices [30,32], cerebellum [33] and primary and association auditory cortices [6].

Third, just as a visual or an auditory representation of an action can lead to the reinstatement of its motor description, the motor representation of the action (the activity pattern unfolding in motor cortices while the action is performed) should activate the pertinent higher-order CDZ (i.e. MNs) and, via divergent back projections, retro-activate sensory representations of the action (e.g. visual, auditory and somatosensory). This prediction has been confirmed experimentally: when subjects perform actions, there is activation of temporal sensory association cortex even when the subjects can neither see nor hear their own movements [35,36].

Finally, if MNs operate as CDZs, the cross-modal associations they code should be subject to modulation by experience. This has been elegantly illustrated by the work of

Heyes and colleagues [37,38]. After a short period of ‘incompatible training’, during which subjects perform movements of the little finger while observing index-finger movements, the motor cortex implicated in movements of the little finger is no longer preferentially activated when the subjects observe such movements but when they observe index-finger movements [37]. Similar ‘incompatible training’ leads to hand-specific activations in MN areas upon observing foot actions [38]. These findings underscore the fact that the cross-modal associations coded by MNs are established by a learning process, just as the CDZ framework predicts, rather than being an intrinsic and fixed property of the system.

### Grandmother neurons are convergence–divergence zones

The aforementioned studies provide solid evidence that processing of an object, both during perception and recall, relies on distributed neural activity in early sensorimotor cortices. We propose that it is this distributed activity pattern, rather than activity in neurons at the top of the processing cascade, that enables us to experience explicit mental images when we perceive or recall objects and events. If a grandmother neuron is defined as a cell whose sole activity permits explicit mental images of objects and events, then we believe grandmother neurons do not exist. We note, however, that a less stringent definition of the term might apply; Kreiman, Koch and Fried [39] have shown that there are, indeed, cells in the anterior medial temporal lobe that respond to unique objects, be they perceived or recalled, with both high specificity and high invariance. Thus, if a grandmother neuron is defined more liberally as a cell whose activity correlates with the presence of a specific object, then the existence of such neurons has been all but proven. The specific and invariant responses of these cells attest to a high level of signal convergence in their afferent connectivity and, therefore, demonstrate one of the two key properties of a convergent–divergent neural architecture. However, activating these neurons does not complete the task; in other words, it would enable us neither to recognize our grandmother nor to remember her. Reinstating a substantial part of the collection of explicit maps which, in their entirety, represent the meaning of an object (or a person in this case), calls for the second key attribute of the CDZ architecture, namely, divergent back projections that establish, in early sensorimotor cortices, the kind of activity patterns for which there is ample evidence in the studies we have reviewed. We suggest that grandmother neurons, like MNs, act as CDZs, which enable the time-locked multiregional retro-activation of explicit maps in early sensorimotor cortices.

### Objections and unanswered questions

Several of the studies discussed above demonstrate that early cortices of a certain sensorimotor modality may be activated in the absence of intramodal perceptual stimulation or overt movement. This finding lends strong support to the concept of multiregional retro-activation. Nevertheless, some objections can be raised relative to our interpretations.

One might suggest, for example, that the cross-modal activity patterns observed in early sensorimotor cortices reflect non-specific excitatory states induced by top-down modulatory processes such as those referred to in **Box 1**, rather than stimulus-specific associations. For example, in the visuo-haptic matching task described earlier [12,13], the activity elicited by the visual cue in primary somatosensory cortex would merely reflect non-specific, 'preparatory' activation, given that the monkey expects to touch the haptic sample soon. However, as noted, part of the recorded somatosensory neurons displayed selectivity to either the horizontal or the vertical haptic samples, and of those the vast majority (>80%) also responded selectively to the corresponding visual cue (horizontal or vertical stripes). This finding is not compatible with a non-specific activation of somatosensory cortices. Along the same lines, motor activations elicited by action observation have been shown to be somatotopic; in other words, observing mouth, hand and foot actions elicits activity in the corresponding areas of the motor cortices [34]. Furthermore, it has been shown that when a human subject observes hand and arm movements, motor potentials evoked by stimulating the observer's motor cortices are selectively enhanced in the muscles the observer would recruit to execute the observed movements himself [40]. These observations suggest that the activation pattern in a subject's motor cortices specifically reflects the contents of the visual event the subject observes.

As a further objection, one could argue that, although stimulus specific, the activations in early cortices observed during imagery and during perceptual processing of stimuli in other modalities might be purely epiphenomenal. Accordingly, integrated mental images would arise from the activity of neurons in higher-order association cortices (grandmother neurons, in the extreme view), and the activations in early sensorimotor cortices would merely reflect a non-functional byproduct. The strongest arguments against such a view come from lesion studies. As mentioned, the generation of integrated mental images is not impaired after damage to high-order association cortices [1]; damage to early sensory cortices, by contrast, is associated with a variety of devastating deficits in image generation, ranging from a complete absence of images in a certain modality to more selective deficits depending on the size and location of the lesion [14,21]. Further evidence against the view that the activity patterns in early sensorimotor cortices would not be causally related to image generation is provided by the studies we have reviewed: first, disrupting early visual cortices by TMS impairs visual mental imagery [18]; second, TMS targeted at a specific part of the visual cortex impairs performance in a tactile orientation discrimination task [11]; and third, processing of visual stimuli in a mental rotation task is affected when TMS is used to disrupt primary motor cortices [24].

In brief, we provide evidence that early cortices of a given sensorimotor modality can be activated in the absence of direct perceptual engagement or motor output. We suggest that the activations in early cortices (i) represent stimulus-specific content rather than a non-specific modulatory effect and (ii) are functional rather than epiphenomenal.

## Box 2. Questions for future research

- Will future studies in experimental neuroanatomy permit characterization in more detail of the reciprocal connectivity patterns between early and association cortices of different sensory modalities? Will such studies confirm the convergent-divergent connectivity scheme suggested here?
- According to the CDZ framework, a sensory stimulus that is presented in one modality but has meaning in a different modality should evoke activations according to a well-specified temporospatial processing sequence. When observing a lip movement, for example, this sequence should be: early visual cortices → visual association cortices → multimodal association cortices → auditory association cortices → early auditory cortices. Will electrophysiological recordings (single-unit or field-potential) provide evidence for (part of) this activation sequence?

## Concluding remarks

The CDZ framework posits two somewhat separate 'brain spaces'. In one, explicit maps of objects and events are constructed during perception and re-constructed during recall. In either condition, there is a manifest correspondence between the properties of the object and the map. The other space holds dispositions rather than maps, that is, implicit formulas for how to reconstruct maps elsewhere. The explicit map space is constituted by the aggregate of early sensorimotor cortices. The implicit, dispositional space is constituted by the aggregate of association cortices. The two spaces point to different ages in brain evolution, one in which dispositions sufficed to guide adequate behavior and another in which sheet-like maps give rise to images, the currency of minds.

Images can be experienced during perception and during recall. It would be impossible to store the maps underlying the images in their original sheet-like format given that the early sensory cortices (the only locus with the necessary anatomical specifications for this task) are permanently constructing updated maps about the current environment. The novelty in brains such as ours is not merely the emergence of maps but also the reciprocal connections between the two brain spaces described earlier, such that maps can be recorded in dispositional form and dispositions can be used to reconstruct maps. Dispositions are a space-saving mechanism for information storage; however, to be represented as mental images (conscious mental images, in particular) the dispositions have to unfold into maps again. Sheet-like maps as they are present in early sensory cortices are the only format information can assume if it is to become part of our minds (see **Box 2** for questions for future research).

## Acknowledgements

Owing to space limitations, we could not discuss all the relevant literature and we apologize to those whose work has not been considered. We thank H. Damasio, M.H. Immordino-Yang and S. Wong for comments on previous versions of this manuscript. K.M. is supported by the Swiss National Science Foundation ([www.snf.ch](http://www.snf.ch)). A.D. is supported by the Mathers Foundation ([www.mathersfoundation.org](http://www.mathersfoundation.org)) and the National Institutes of Health ([www.nih.gov](http://www.nih.gov); 5P50NS019632–25).

## References

- 1 Damasio, A.R. (1989) Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition* 33, 25–62

- 2 Barsalou, L.W. (2008) Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645
- 3 Simmons, W.K. and Barsalou, L.W. (2003) The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cogn. Neuropsychology* 20, 451–486
- 4 Rockland, K.S. and Pandya, D.N. (1979) Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. *Brain Res.* 179, 3–20
- 5 Van Hoesen, G.W. (1982) The parahippocampal gyrus: new observations regarding its cortical connections in the monkey. *Trends Neurosci.* 5, 345–350
- 6 Calvert, G.A. *et al.* (1997) Activation of auditory cortex during silent lip reading. *Science* 276, 593–596
- 7 Kiefer, M. *et al.* (2008) The sound of concepts: Four markers for a link between auditory and conceptual brain systems. *J. Neurosci.* 28, 12224–12230
- 8 González, J. *et al.* (2006) Reading *cinnamon* activates olfactory brain regions. *Neuroimage* 32, 906–912
- 9 Hagen, M.C. *et al.* (2002) Tactile motion activates the human middle temporal/V5 (MT/V5) complex. *Eur. J. Neurosci.* 16, 957–964
- 10 Sathian, K. *et al.* (1997) Feeling with the mind's eye. *Neuroreport* 8, 3877–3881
- 11 Zangaladze, A. *et al.* (1999) Involvement of visual cortex in tactile discrimination of orientation. *Nature* 401, 587–590
- 12 Zhou, Y.-D. and Fuster, J.M. (1997) Neuronal activity of somatosensory cortex in a cross-modal (visuo-haptic) memory task. *Exp Brain Res.* 116, 551–555
- 13 Zhou, Y.-D. and Fuster, J.M. (2000) Visuo-tactile cross-modal associations in cortical somatosensory cells. *Proc. Natl. Acad. Sci. U. S. A.* 97, 9777–9782
- 14 Kosslyn, S.M. *et al.* (2001) Neural foundations of imagery. *Nat. Rev. Neurosci.* 2, 635–642
- 15 Pylyshyn, Z. (2003) Return of the mental image: are there really pictures in the brain? *Trends Cogn. Sci.* 7, 113–118
- 16 Kosslyn, S.M. *et al.* (1995) Topographical representations of mental images in primary visual cortex. *Nature* 378, 496–498
- 17 Slotnick, S.D. *et al.* (2005) Visual mental imagery induces retinotopically organized activation of early visual areas. *Cereb. Cortex* 15, 1570–1583
- 18 Kosslyn, S.M. *et al.* (1999) The role of area 17 in visual imagery: convergent evidence from PET and rTMS. *Science* 284, 167–170
- 19 Lotze, M. and Halsband, U. (2006) Motor imagery. *J. Physiol. (Paris)* 99, 386–395
- 20 O'Craven, K.M. and Kanwisher, N. (2000) Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *J. Cogn. Neurosci.* 12, 1013–1023
- 21 Farah, M.J. (1988) Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psychol. Rev.* 95, 307–317
- 22 Shepard, R.N. and Metzler, J. (1971) Mental rotation of three-dimensional objects. *Science* 171, 701–703
- 23 Richter, W. *et al.* (2000) Motor area activity during mental rotation studied by time-resolved single-trial fMRI. *J. Cogn. Neurosci.* 12, 310–320
- 24 Ganis, G. *et al.* (2000) Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cereb. Cortex* 10, 175–180
- 25 Damasio, A. and Meyer, K. (2008) Behind the looking-glass. *Nature* 454, 167–168
- 26 Gallese, V. *et al.* (1996) Action recognition in the premotor cortex. *Brain* 119, 593–609
- 27 Rizzolatti, G. and Craighero, L. (2004) The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192
- 28 Kohler, E. *et al.* (2002) Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297, 846–848
- 29 Keysers, C. *et al.* (2003) Audiovisual mirror neurons and action recognition. *Exp. Brain Res.* 153, 628–636
- 30 Raos, V. *et al.* (2007) Mental simulation of action in the service of action perception. *J. Neurosci.* 27, 12675–12683
- 31 Tkach, D. *et al.* (2007) Congruent activity during action and action observation in motor cortex. *J. Neurosci.* 27, 13241–13250
- 32 Blakemore, S.-J. *et al.* (2005) Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain* 128, 1571–1583
- 33 Lahav, A. *et al.* (2007) Action representation of sound: audiomotor recognition network while listening to newly acquired actions. *J. Neurosci.* 27, 308–314
- 34 Buccino, G. *et al.* (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13, 400–404
- 35 Iacoboni, M. *et al.* (2001) Reafferent copies of imitated actions in the right superior temporal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 98, 13995–13999
- 36 Gazzola, V. *et al.* (2006) Empathy and the somatotopic auditory mirror system in humans. *Curr. Biol.* 16, 1824–1829
- 37 Catmur, C. *et al.* (2007) Sensorimotor learning configures the human mirror system. *Curr. Biol.* 17, 1527–1531
- 38 Catmur, C. *et al.* (2008) Through the looking glass: counter-mirror activation following incompatible sensorimotor learning. *Eur. J. Neurosci.* 28, 1208–1215
- 39 Kreiman, G. *et al.* (2000) Imagery neurons in the human brain. *Nature* 408, 357–361
- 40 Fadiga, L. *et al.* (1995) Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73, 2608–2611
- 41 Churchland, P.S. *et al.* (1994) A critique of pure vision. In *Large-Scale Neuronal Theories of the Brain* (Koch, C. and Davis, J.L., eds), pp. 23–60, MIT Press