

digestion of sushi in the gut microbes of Japanese people [11].)

The authors find that alginate and alginate lyase activities mirror gene content and dosage both quantitatively and qualitatively (in terms of useable alginate polymer length) and that some strains (with shorter lag times in growth experiments) more actively excrete ('broadcast') degradative enzymes. Possibly this is a variable property of the gene products themselves (different export and tethering characteristics), indicating acquisition of new (not just more) function through xenology, possibly from outside the vibrio populations studied. In this case, we still might ask whether in the end duplication and divergence are not the creative force (Figure 1). It could be that prokaryotic gene duplicates not under selection for increased gene dosage are just occasionally held onto long enough to differentiate functionally. This being rare — and HGT within and between species being frequent — it will be the case that in most genomes harboring two functionally differentiated copies, these will be xenologs, not paralogs. And if HGT is indeed more frequent than duplication [4], this will be true even without functional differentiation.

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Visual Neuroscience: Seeing Causality with the Motor System?

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Understanding how humans perceive cause and effect in visual events has long intrigued philosophers and scientists. A new study in primates reveals the neural correlates of perceived causality at the single-cell level, but in an unexpected place — the motor system.

Clap your hands: we have all learned how to do this when we were very young, babies in fact, most likely from our parents or siblings. Clapping is a milestone for the developing infant that, beyond motor coordination, involves the perception of causality: two hands, stopping each other in mid-flight, cause that unmistakable sound. The inference of causality provides structure to a dynamic visual world, is crucial for successful manipulations of it (Figure 1), and shapes the way we describe it: she pulls the cloth off the table; he kicks the door shut; the waves rock the boat. Indeed, babies as young as 6 or 7 months of age appear to discern causality in abstract visual displays such as the launching stimulus, in which one object is seen to cause another object to move by crashing into it [1,2]. These findings fueled debates started by the father of the field, the Belgian psychologist Albert Michotte [3]. On the basis of spontaneous reports of subjects seeing launching stimuli, Michotte proposed that the detection of causality is an immediate, visual process, rather than a reflective, cognitive

one, and that it is innate, rather than acquired through learning [4,5]. In a new study reported in this issue of *Current Biology*, Caggiano *et al.* [6] discovered neurons that appear to encode visual events with specific causal properties, such as spatiotemporal contingencies. Unexpectedly, these neurons are in the motor cortex, giving a new twist to how we think about the mechanisms giving rise to the perception of causality.

Caggiano *et al.* [6] recorded from neurons in area F5 of the primate brain, which contains large numbers of so-called mirror neurons that respond to both performing a certain action as well as seeing the same action performed. Their monkeys viewed short and highly controlled videos of naturalistic actions. One version of the video (the grasping version) begins with a pepper lying on a table, and then a hand moves into the frame, picks up the vegetable, and removes it from view. The second version (the placing version) is the same video played backwards, showing a hand moving into view and putting down the



Figure 1. Understanding causality.

Understanding that our actions have an impact on the environment is a crucial part of development. Here, the boy appears to understand that he needs to reach for the bowl and pull it closer. A new study [6] suggests that the motor system is also involved in detecting causality in abstract visual events, such as seeing one object pulling along another.

pepper before moving out of view again. In a first step, the authors identified F5 neurons that responded selectively to either the grasping or the placing version of this video — as well as to grasping and placing actions performed by the monkey. Indeed, each of these neurons would systematically fire during one part of the observed action — for example, the hand moving towards the pepper, or the hand lifting the pepper — and clearly differentiate between grasping and placing. Collectively, a population of neurons thus integrated and encoded the entire action sequence.

Having set the stage in Experiment 1, Caggiano *et al.* [6] conducted a second experiment, which revealed the study's core findings. In this experiment, they created abstract versions of the videos by replacing both the hand and the pepper with simple, colored discs (of similar size as the hand and the pepper) that followed the exact same movement trajectories. Despite this rather strong visual manipulation of the stimulus material, the observed neural responses were barely altered compared to the original videos: neurons that responded selectively to grasping would also fire most vigorously during videos of a moving disc approaching a stationary one until both discs partially overlapped and left the screen in concert. Likewise, neurons that were selective for placing actions would

also fire most during a video of a pair of discs moving into the screen before one would move back out, leaving the other behind. Indeed, the differences in neural firing patterns between the naturalistic actions and their abstract counterparts were negligible in the vast majority of neurons. Instead of encoding grasping or placing *per se*, it seems, these neurons abstract spatiotemporal properties from the stimulus sequence.

While this result is interesting in itself, it suggested an even more intriguing possibility: F5 neurons might encode the causal structure that an action implies. The idea is that the videos used in the experiments (see Supplemental Movie 1 in [6]) generate the perception of causal relations between two stimuli: a disc picks up another disc, or puts it in a new place. In spirit, therefore, these causal events are similar to the launching stimuli introduced by Michotte and used in most subsequent studies of the perception of causality [1–5]. Luckily (at least from an experimenter's perspective), causality is a delicate percept that vanishes reliably when we alter the expected spatiotemporal contingencies of an event [3–5]. To test the possibility that responses of F5 neurons are specific to the causal relation inherent to a grasping or placing action, therefore, Caggiano *et al.* [6] recorded responses from the same set of neurons in a number of additional conditions. Each of these conditions was expected either to diminish the perceived causality or to leave it intact. It turned out that any manipulation that reduced perceived causality — such as preventing contact between the two discs or just showing the initial motion of the hand — also reliably altered the response of the neurons. In contrast, changing properties that do not influence perceived causality — such as inverting the colors of the discs — did not affect these neurons' responses. Together, these findings suggest that the critical feature driving these responses in F5 is the causal relation between the two movements, not any other particular feature of the visual event.

In at least one respect, however, activity in F5 does not appear to match human perception of causality, and that has to do with adaptation. Adaptation is a mechanism that is common to most (if not all) visual processes: after one stimulus feature is presented repeatedly,

observers' perception becomes biased away from that feature, and the gain of neural populations processing that feature is reduced (they fire less vigorously). For instance, we see a green patch hovering on a white wall after staring at something red, and we see stationary objects as expanding after staring at an inwardly contracting spiral. Adaptation thus strongly affects all aspects of how we see [7]. Indeed, after viewing many repetitions of causal events (collisions of discs that launch each others' movements), viewers perceive causality less often in similar displays, and that aftereffect is spatially specific to the adapted retinotopic location [8,9]. Thus, much as prolonged exposure to color or motion stimuli gives rise to strong negative visual aftereffects, prolonged exposure to causal events results in perceptual aftereffects, demonstrating the existence of spatially-specific visual mechanisms that process causality [10].

Curiously, F5 neurons show some spatial selectivity in a retinotopic reference frame [11]. But in a previous paper, Caggiano and colleagues [12] studied neural adaptation to the same naturalistic stimuli they used in their new study and found that F5 neurons — by and large — do not reduce their responses following repeated presentation of the same stimulus. What does the difference in findings between neural and perceptual adaptation tell us about the role of area F5 in the perception of causality? John Frisby [13] famously called perceptual adaptation the psychologists' micro-electrode; but in comparison to neurophysiologists, psychologists know little about their microelectrode's target area. Several brain areas other than F5 have been implicated in the processing of causal stimuli [14,15], including some that are retinotopically organized. A possible key area for the detection of causality is the superior temporal sulcus (STS), which provides input to area F5. Interestingly, whereas repeated presentations of the same (causal) action did not cause F5 neurons to reduce their firing, local field potentials recorded in the same area showed clear signs of adaptation [12]. Local field potentials, in turn, are thought to relate strongly to synaptic activity [16], and it seems possible that input signals coming from STS to F5 are indeed adapted. Caggiano *et al.* [12] speculated,

therefore, that this adaptation is compensated for (that is, the neural response gain is up-regulated) by local circuitry in F5.

Beyond those theoretical possibilities, there are a number of obvious differences between the experimental procedures used in the behavioral [8,9] and neurophysiological [12] studies (launching *versus* grasping/placing; hundreds of repetitions *versus* a single repeat). Future studies will be able to build on Caggiano *et al.*'s [6] findings by using Michotte-type displays while recording from area F5, by adapting neurons on longer time scales (see also [17]), and ultimately, by recording from, selectively stimulating, or reversibly inactivating neurons in a range of brain areas that may contribute causally to the perception of causality (such as STS or area V5) [14,15].

With their new study, Caggiano *et al.* [6] have thus paved the way for understanding the neural correlates of the perception of causality at the single-cell level. By starting this endeavor in area F5, they have put the motor system more centrally on the map. Very few authors had previously proposed links between the hand movement system and the perception of causality [18–20]. Caggiano *et al.*'s [6] new data do not exclude a key role of the visual system in the detection of causality in visual events. Instead, they suggest that the motor system contributes to the recognition of causal actions [19]. The jury is still out on whether the motor system is crucial to shaping our perception of causality in visual events, but experience based on body movements may provide templates to which visual events could be matched [19,20]. Caggiano *et al.*'s [6] new results, therefore, will contribute to more comprehensive theories of the perception of causality and inform our understanding of its development in infants and across the lifespan.

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Sensory Development: Brief Visual Deprivation Alters Audiovisual Interactions

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Two recent studies have independently demonstrated that short periods of visual deprivation early in human development can have long-term functional consequences on sensory perception and on the balance between auditory and visual attention.

We live in a multisensory world. We simultaneously experience visual and auditory inputs which can often be combined with tactile, olfactory, or gustatory sensations. Elucidating how

these senses develop and interact is thus critical to our understanding of brain development and plasticity. When sensory systems have developed normally, these multisensory percepts are

