cell lineage at the expense of the other during stem/progenitor cell renewal.

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Body Perception: Intersensory Origins of Self and Other Perception in Newborns

Self-perception involves integrating changes in visual, tactile, and proprioceptive stimulation from self-motion and discriminating these changes from those of other objects. Recent evidence suggests even newborns discriminate synchronous from asynchronous visual-tactile stimulation to their own body, a foundation for self-perception.

L.E. Bahrick

"Information about the self accompanies information about the environment, and the two are inseparable. Egoreception accompanies exteroreception, like the other side of a coin. Perception has two poles, the subjective and objective, and information is available to specify both. One perceives the environment and coperceives oneself"

J.J. Gibson [1] (p. 126)

The world provides a richly structured array of continuously changing multimodal stimulation to all our senses. Despite the fact that our information about the world is dynamic and arrives through distinct sensory channels, we perceive ourselves as coherent entities, situated in a stable world of unitary objects and events. How and when we develop the ability to coordinate stimulation across the senses such that we perceive the self and the objects and events in the world as distinct, unitary multimodal entities is a question that has intrigued philosophers and scientists for centuries, dating as far back as Aristotle. A recent study by Filipetti et al. [2], reported in this issue of

Current Biology, adds a new piece to this puzzle. It suggests that a fundamental form of this ability is present in newborn infants. Newborns detect visual-tactile synchrony in movements directed to their own body and discriminate synchrony from visual-tactile asynchrony. Synchrony detection is known to be a cornerstone of perceptual development, a key to linking stimulation across the senses, and a foundation for distinguishing the self from other objects and events in the world [3,4].

The past several decades have witnessed an explosion of research on intersensory and synchrony perception, catalysed in large part by James and Eleanor Gibson's [1,5,6] ecological approach to perception and perceptual development. Instead of posing a problem for perception, as argued by prevailing theories, the Gibsons proposed that the different forms of sensory stimulation and their overlap provide an important basis for perceiving a unified self situated in a world of unified multimodal objects and events. The senses work in concert



to detect 'invariant' aspects of stimulation, including 'amodal invariants', aspects such as synchrony, rhythm, and intensity patterns that are specified across multiple sensory channels. Research now indicates that even young infants are skilled at detecting a host of amodal invariants, including synchrony, considered to be the most fundamental for organizing and promoting early perceptual development [3,7,8]. Temporal synchrony has been considered the 'glue' that binds stimulation across the senses and the gateway to perceptual processing [3,4]. Sensitivity to synchrony across the senses allows even naïve perceivers to experience unitary multimodal events and to separate stimulation originating from the self versus that arising from others.

Much of this research has focused on infant intersensory perception of external events, such as a person speaking or an object striking a surface. Infants are skilled at perceiving synchrony uniting auditory and visual stimulation from these events [3,4,8,9]. Much less is known about infants' intersensory perception of information generated by the self and self-motion. though the self provides one of the first and most reliable sources of intersensory synchrony. Proprioceptive feedback from body motion, such as kicking the legs or moving the hand against a surface, is perfectly synchronized with the accompanying visual and tactile consequences of this motion and this multimodal synchrony is continuously available from birth onward. Even fetuses experience synchronized proprioceptive and tactile stimulation from self-motion. Research has demonstrated that infants detect this proprioceptivevisual synchrony generated by self-motion. For example, five-montholds discriminate between a live (synchronous) versus a pre-recorded (nonsynchronous) video display of their own legs kicking or a video of another infant's legs (nonsynchronous) and prefer to watch the nonsynchronous stimulation [10]. Visual stimulation synchronous with proprioceptive feedback specifies the self whereas visual stimulation asynchronous with proprioceptive feedback specifies not-self or a social partner [10]. Thus, body related synchrony detection is evident in infancy and is fundamental for distinguishing self from other.

Even newborns demonstrate sensory integration and synchrony detection in perception of both external events and stimulation from the self. They show visual-tactile transfer in object exploration [11] and detection of audiovisual synchrony uniting facial and vocal displays [12]. They learn audiovisual pairings when they are contingent upon their own visual fixations but not when they are noncontingent [13]. Newborns coordinate proprioceptive with visual stimulation in reaching [14], discriminate self-touch from the touch of another person [15], and even show auditory-visual-proprioceptive integration by imitating facial expressions in the presence of synchronous, but not asynchronous, audiovisual speech [16].

Synchrony detection is also key to self-other perception because it unifies stimulation across the senses [3,4,7]. It binds multimodal stimulation from our body movements across the senses and separates it from the stimulation generated by other objects and events that are not synchronous with self-movement. As noted in the quote by Gibson [1], "one perceives the environment and coperceives onself": self and not-self are two sides of the same coin. In fact synchrony perception is so fundamental for unitizing stimulation that adults perceive illusions based on synchrony, for stimulation from both external events and from the self. In the 'ventriloquism effect' [17], by synchronizing the movements of the puppet's mouth and body with his own speech sounds, the ventriloguist creates the illusion that the puppet is speaking, even though the puppet is not co-located with the source of the sound. Similarly, adults show a 'rubber hand illusion' [18] demonstrating the power of synchrony to unite stimulation across the senses in the domain of body awareness. If an adult's hand is stroked in synchrony with that of a visible rubber hand, adults report feeling that the rubber hand is part of their body. These illusions disappear if the visual-tactile or visual-auditory stimulation is delivered asynchronously.

The study by Filipetti *et al.* [2] now indicates that even newborn infants detect visual-tactile synchrony similar to that depicted in the rubber hand illusion. Newborns received rhythmic stimulation from a brush stroking their cheek. At the same time, they viewed two video displays of a brush stroking an infant's cheek. One was synchronized with the tactile stimulation experienced by the infant and the other was asynchronous. In one experiment, in which the video displays were upright, newborns preferentially viewed the video synchronized with the tactile stimulation, providing the first demonstration of newborn detection of visual-tactile synchrony generated from stimulation to their own body. This finding leaves ripe for investigation questions regarding the origins of this ability to detect body-related synchrony. Given that the neural architecture for synchrony detection is intact in neonates, for both body-related synchrony and synchrony generated by external events, the nature of specific fetal experience that contributes to the development of this architecture is a fertile ground for future investigation.

In the second experiment, the video displays were inverted, and newborns no longer showed a preference for synchrony, Filipetti et al. [2] conclude that infants were less likely to relate the inverted displays to their own body and, thus, this condition demonstrates a preference for synchrony between observed and felt actions "only in the context of stimuli that are related to their own bodies". Interpreting the findings of this second study, however, is less straight forward, given that neonates have very limited experience with upright versus inverted faces. There are a number of alternative hypotheses for the failure of newborns to detect synchrony in the inverted condition that suggest why synchrony detection might be more difficult for inverted faces (rather than perceived as less 'body related'). They include recruitment of different attentional strategies for upright versus inverted faces, a possible mismatch in the spatial alignment of the visual and tactile stimulation in the inverted condition (for example, any upward or downward component to the stroking trajectory would cause the visually given upward/downward movements to be spatially aligned with felt movements in the upright, but misaligned in the inverted condition), or a domain general bias in neonates for patterns with more elements in the upper portion [19].

Another intriguing question, ripe for future investigation, is when and

how does the visual, tactile, and proprioceptive stimulation generated by self-movement come to specify the self. We do not know when infants develop 'self-recognition' and perceive the synchrony related to their own body movements as belonging to the self. The present studies and those cited above demonstrate that very young infants detect information fundamental to self-recognition. They distinguish between stimulation that is synchronous vs. asynchronous with self-motion and self-touch. Although it is tempting to infer that infants attribute body-related synchrony to the self and are aware that "this is me!", further research will be necessary to explore this intriguing developmental process. Infants likely show a growing awareness of the bodily self, with early differentiation of self from other stimulation and much development thereafter, prior to the age of 15-18 months, when they demonstrate self-recognition according to the well-known rouge test [20].

The Filipetti *et al.* [2] study has added to the growing picture of newborn intersensory capabilities and demonstrates remarkably early sensitivity to body-related visual-tactile synchrony. Together with prior studies of infant sensitivity to proprioceptive-visual synchrony, this raises intriguing questions about the developmental origins of these intersensory skills. Significant prenatal experience is likely involved in developing these skills and the neural architecture to support them and significant postnatal experience is certainly required to refine, develop, and calibrate the senses for developing a richer, more complete sense of the body in space and its relation to other objects and events in the world.

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Evolution: Sex or Survival

A classic paradox in sexual selection is how sexual traits under strong directional selection maintain underlying genetic variation. A new study has found that in Soay sheep a trade-off between reproductive success and survival maintains variation in horn size.

James Howie¹, Andrew Pomiankowski^{1,2,*}, and Alison J. Cotton^{1,2}

Sexual selection provides a compelling evolutionary explanation for the diverse array of sexual ornaments and mating behaviours observed in nature. Yet, at the heart of this theory lies a paradox: male-male competition and female mate preferences cause strong directional selection on sexual characters [1,2]. So, one might expect that allelic variation underlying traits with such important fitness effects would rapidly spread to fixation and denude genetic variation. But empirical evidence shows this is not the case. Traits subject to sexual selection have substantial genetic variation, more so than most ordinary morphological and behavioural traits [2]. A number of plausible hypotheses have been put forward as resolutions of this so-called 'lek paradox', principally relating to genic capture — trait expression depending on multiple genes that underlie an individual's condition [2,3] — and sexually antagonistic selection on alleles that increase the fitness of one sex while decreasing that of the other [4]. However, direct empirical tests remain rare. In a new study, Johnston *et al.* [5] have gone a long way to understanding the major components of genetic variation in horn size, a sexually selected trait in Soay sheep (*Ovis aries*), and turn their findings into a novel solution to the lek paradox.

Soay sheep are a feral population of primitive domestic sheep living on the remote island of Hirta in the St. Kilda archipelago, off the West Coast of Scotland. They have been intensively studied for the last 30 years, with genetic data being collected since 1985

