

[10,11]. However, it seems that the burden of proof is on Firestone and Scholl to design and fully report a study that demonstrates how fashion and/or transportation pop-out is 'entirely analogous' to moral pop-out.

Concluding Remarks

We leave it to you, the reader, to evaluate Firestone and Scholl's claims. We fail to see how hitting a small child does not pertain to morality, knowing that expectations of justice affect attention is unexciting, or formal claims about similarity can be made without randomly assigning people to conditions or even presenting similar data. Clearly, moral perception is a provocative topic. Perhaps the only thing we can agree on is that more research is needed.

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References

- Gantman, A.P. and Van Bavel, J.J. (2015) Moral perception. *Trends Cog. Sci.* 19, 631–633
- Firestone, C. and Scholl, B.J. (2015) 'Moral perception' reflects neither morality nor perception. *Trends Cog. Sci.* 19, 631–633
- Anderson, E. et al. (2011) The visual impact of gossip. *Science* 332, 1446–1448
- Uhlmann, E.L. et al. (2015) A person-centered approach to moral judgment. *Pers. Psychol. Sci.* 10, 72–81
- Callan, M.J. et al. (2013) Eye movements to audiovisual scenes reveal expectations of a just world. *J. Exp. Psychol. Gen.* 142, 34–40
- Ginges, J. et al. (2007) Sacred bounds on rational resolution of violent political conflict. *Proc. Natl. Acad. Sci. U.S.A.* 104, 7357–7360
- Granoit, Y. et al. (2014) Justice is not blind: visual attention exaggerates effects of group identification on legal punishment. *J. Exp. Psychol. Gen.* 143, 2196–2208
- Gantman, A.P. and Van Bavel, J.J. (2014) The moral pop-out effect: Enhanced perceptual awareness of morally relevant stimuli. *Cognition* 132, 22–29
- Firestone, C. and Scholl, B.J. (2015) Enhanced visual awareness for morality and pajamas? Perception vs. memory in 'top-down' effects. *Cognition* 136, 409–416

- Haidt, J. et al. (1993) Affect, culture, and morality, or is it wrong to eat your dog? *J. Pers. Soc. Psychol.* 65, 613–628
- Rozin, P. (1999) The process of moralization. *Psychol. Sci.* 10, 218–221
- Firestone, C. and Scholl, B.J. (2015) Cognition does not affect perception: evaluating the evidence for 'top-down' effects. *Behav. Brain Sci.* Published online July 20, 2015. <http://dx.doi.org/10.1017/S0140525X15000965>

Forum

Neural Antecedents of Spontaneous Voluntary Movement: A New Perspective

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Fifty years ago, Kornhuber and Deecke first reported their discovery of the *Bereitschaftspotential* [1], or cortical 'readiness potential' (RP) (see Glossary), a slow build-up of scalp electrical potential preceding the onset of subjectively spontaneous voluntary movements (SVMs). The RP was interpreted as 'the electro-physiological sign of planning, preparation, and initiation of volitional acts' [2], implicitly presumed to reflect the consequence of a decision process in the brain. Then, in the early 1980s, Benjamin Libet found that the onset of the RP precedes subjective estimates of the time of the conscious 'urge' to move by 300 ms or more [3] – a result that has since been confirmed at the single-neuron level [4]. This counterintuitive discovery, which we call 'Libet's paradox', led to the view that the conscious decision emerges well after the action has already been initiated unconsciously in the brain, as reflected in the apparent build-up of the RP. While controversy over Libet's findings has churned vigorously for many years, crucial assumptions about the nature of the RP itself have gone unquestioned.

Now a series of new developments has begun to unravel what we thought we knew about the brain activity preceding SVMs.

Glossary

Bounded integration: also known as integration to bound or evidence accumulation, the term refers to a computational model of decision making wherein sensory evidence and internal noise (both in the form of neuronal activity) are integrated over time by one or more decision neurons until a fixed threshold-level firing rate is reached, at which point the animal issues a motor response. In the case of spontaneous self-initiated movement there is no sensory evidence, so the process is dominated by internal noise.

False-positive rate: how often we decide that a movement will occur when in fact it does not.

Neural decision to move: a neural event or state that commits some part of the body to an imminent movement. It is not necessary for this state to be conscious for it to qualify as a 'decision'.

Readiness potential (RP): originally dubbed the *Bereitschaftspotential* by Kornhuber and Deecke [1], the name refers to a slow build-up of scalp electrical potential, measured using (EEG) or electrocorticography (ECoG), preceding the onset of spontaneous self-initiated movements. When measured using magnetoencephalography (MEG) the build-up is referred to as a 'readiness field' and when measured as a change in firing rate in single neurons it is referred to as a 'readiness discharge'.

Time-unlocked forecasting: movement-locked data give us, at each time point $t - \tau$, the probability of the signal at time $t - \tau$ given a movement at t_0 : $p(S_{t-\tau}|M_{t_0})$. Time-unlocked forecasting tells us the probability of a movement at time $t + \tau$ in the future given the signal now and in the recent past: $p(M_{t+\tau}|S_t, S_{t-1}, \dots, S_{t-n})$.

True-positive rate: how often we decide that a movement will occur when in fact it does.

The main new revelation is that the apparent build-up of this activity, up until about 200 ms pre-movement, may reflect the ebb and flow of background neuronal noise, rather than the outcome of a specific neural event corresponding to a 'decision' to initiate movement. In particular, two independent studies, one using electroencephalography (EEG) recordings in humans [5] and the other using single-unit recordings in rats [6], have converged in showing that **bounded-integration** processes, which involve the accumulation of noisy evidence until a decision threshold is reached, offer a coherent and plausible explanation for the apparent pre-movement build-up of neuronal activity. Bounded integration or 'evidence

accumulation' models have been in use for decades in the study of perceptual decision-making and reaction-time tasks and have proven very powerful in accounting for both neural and behavioral phenomena. Only recently, however, has it come to light that if the 'evidence' is absent, or very weak relative to the noise, such models can also be applied to the spontaneous voluntary initiation of movement [5,6].

Schurger *et al.* asked subjects to perform Libet's [3] task, on each trial pressing a button spontaneously without any pre-planning. Subjects were told that they might sometimes be interrupted by an audible 'click', in which case they should press the button as quickly as possible. Using a leaky stochastic accumulator model [the stochastic decision model (SDM)], Schurger *et al.* predicted that shorter response times should occur on trials in which spontaneous neuronal activity happened to be closer to the decision threshold at the time the subjects were interrupted. The resulting EEG data confirmed this prediction. This build-up could not reflect a process of preparation for movement because the clicks were delivered at random times that were not revealed to the subjects in advance. Explanations based on elapsed time or coincidental movement preparation were also excluded. Remarkably, using the same SDM, Schurger *et al.* were also able to fit the shape of the RP and the distribution of waiting times from a separate session where subjects performed the classic Libet [3] task without interruption.

In Murakami *et al.*'s experiment [6], a rat waited for a liquid reward by keeping its nose in a pokehole (the 'waiting station') until an auditory cue was delivered after a variable delay. If the rat waited for the auditory cue, it could pull its nose out of the waiting station and insert it into an adjacent reward port to receive a large reward. However, sometimes the rat grew impatient and spontaneously left the waiting station to move to the reward port before the auditory cue. In these cases

the rat received only a small reward. When conditioning on trials where the rat spontaneously abandoned waiting for the large reward, neurons in the rat's premotor cortex exhibited a gradual build-up preceding the withdrawal from the waiting station and this neural activity was well modeled by the output of a stochastic accumulator. Interspersed among these neurons was a separate subpopulation of neurons whose activity resembled what one would expect if these were the inputs to an accumulator, with trial-by-trial firing-rate variability that correlated with the amount of time the rat waited before spontaneously opting for the smaller reward.

Schurger *et al.* and Murakami *et al.* independently concluded that SVMs rely on the same neural decision mechanism used for perceptual decisions—integration to bound—except that in this case there is no specific external sensory evidence to integrate. In particular, when actions are initiated spontaneously rather than in response to a sensory cue, the process of integration to bound is dominated by ongoing stochastic fluctuations in neural activity that influence the precise moment at which the decision threshold is reached. In this context, time locking to movement onset means time locking to crests in these temporally auto-correlated background fluctuations, which results in the appearance of a slow, nonlinear build-up in the average. This in turn gives the natural but erroneous impression of a goal-directed brain process corresponding to the 'cerebral initiation of a spontaneous voluntary act' ([3], see p. 640). Consistent with this account, Jo *et al.* [7] have recently put forward evidence that the RP results from an unequal ratio of positive and negative potential shifts.

This is not to say that time locking to movement onset necessarily accounts for the entire phenomenon of the slow build-up, although it can account for a sizeable portion of it. Other factors such as anticipation [8], subjective value [9], and even clock monitoring [10] may be involved as well. This interpretation of the data should also

Box 1. The Perils of Movement-Locked Averaging

Imagine that we want to predict the onset of movement by detecting a build-up of neural activity in the supplementary motor area. Our data comprise epochs of neural spiking rates with the last sample aligned to movement onset. Using signal-detection theory we could try to estimate our performance by looking at our **true-positive rate** and our **false-positive rate**. One glaring problem in this example is the absence of non-movement epochs in our data (Figure 1): we have no way of estimating the false-positive rate, which could be quite high given the rarity of movement onsets with respect to typical sampling rates. This indicates the need for **time-unlocked** methods in the study of movement initiation and highlights the difference between a 'prediction' and a 'forecast' [17]. A prediction is a categorical statement about a specific future commitment to act, whereas a forecast is a probabilistic statement about the range of possible future states and the likelihood of each. A slow build-up of neural activity might be useful for forecasting even if it is not a particularly good predictor, because movement is more likely when neural activity in the relevant populations is waxing rather than waning.

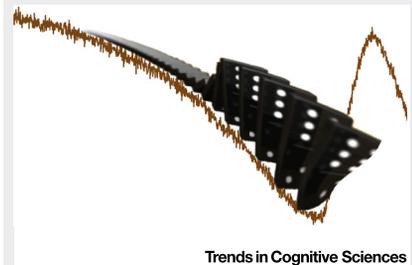


Figure 1. Schematic of Readiness Potential with Falling Dominoes. Extracting data epochs time locked to movement onset can give the impression of a process that began far back in time with the specific purpose of triggering a movement, even if the ongoing fluctuations tending toward the decision threshold are in fact largely stochastic and undirected.

not be taken to require that the behavior be completely stochastic (e.g., a foot movement sometimes resulting when someone is in a state of intending to produce spontaneous hand movements). Certain parameters, such as the movement type, may be fixed by a prior decision to perform the instructed task, which may in turn channel the neural activity leading up to the decision threshold toward a specific effector (Box 1).

This account departs dramatically from the longstanding assumptions about the

Box 2. Philosophical Implications

Many have found Libet *et al.*'s results so striking because they appear to clash with our common-sense view of action initiation. However, the novel interpretation of the RP that the SDM provides actually suggests a close correspondence between the two. When one forms an intention to act, one is significantly disposed to act but not yet fully committed. The commitment comes when one finally decides to act. The SDM reveals a remarkably similar picture on the neuronal level, with the decision to act being a threshold-crossing neural event that is preceded by a neural tendency toward this event.

In addition, dropping the problematic theoretical assumption that a decision to act cannot occur without being conscious also helps to dispel the apparent air of 'paradox' surrounding these findings. As with other types of mental occurrence, the decision to initiate an action can occur before one is aware of it. So we can identify the neural initiating event with a decision that we may become aware of only a brief instant later. All this leaves our commonsense picture largely intact.

Finally, distinguishing between the decision to act and the earlier forming of an intention fits well with the distinction (Box 1) between a prediction and a forecast. If our concern is merely forecasting, what is relevant is the less-committed event of an intention's forming, which we identify with the neural tendency. If our concern is prediction, we should focus on the later event of deciding, which we identify with the crossing of the threshold.

nature of the RP and so calls for a reevaluation and reinterpretation of a large body of prior work. One important consequence is that we must reconsider what previous findings appeared to tell us about our subjective sense of action initiation. Surprisingly, the tenets of the SDM fit remarkably well with our intuitive pre-theoretic views of action initiation and therefore pave the way for a radically new approach to the study of SVM (Box 2). Convergent evidence including Libet's own [3,11,12] indicates roughly 150–200 ms before movement onset as the time of the neuronal commitment to move – and this is indeed the time at which subjects claim to have felt the urge to move when asked to report it [3,5]. What is particularly intriguing about this new

perspective is that it predicts that an event-preceding build-up of intrinsic activity should be a very general phenomenon not necessarily limited to bodily movements [13] and in no way unique to mammals or even vertebrates. In line with this prediction, crayfish were recently shown to exhibit a slow build-up in neural activity preceding spontaneous transitions from rest to foraging [14], with a temporal profile very similar to that found in humans and rats. The classical model can only cast a blank stare at these data, but the SDM predicts them. The only assumption required is that the spectral properties of intrinsic neuronal activity should be similar across vertebrate and invertebrate phyla, which appears to be the case [15,16].

We may have been wholly wrong in our assumptions about the nature of the brain activity that precedes voluntary movement, for 50 years measuring, analyzing, and mapping what may turn out to be a reliable accident: the cortical RP. This new avenue of research brings SVMs into the domain of bounded-integration models of decision making, previously applied primarily to perceptual decisions, and bridges that discipline with the study of intrinsic fluctuations in brain activity [16]. These two fields forge an unexpected and promising theoretical unity, providing a new framework for the study of action initiation with the potential to transform the way neuroscientists, psychologists, and philosophers of mind approach the study of spontaneously initiated voluntary movement.

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References

- Kornhuber, H.H. and Deecke, L. (1965) Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. [Changes in brain potentials with willful and passive movements in humans: the readiness potential and reafferent potentials]. *Pflügers Archiv*, 284, 1–17 (in German)
- Kornhuber, H.H. and Deecke, L. (1990) Readiness for movement – the *Bereitschaftspotential* story. *CC Life Sci*, 33, 14
- Libet, B. *et al.* (1963) Time of conscious intention to act in relation to onset of cerebral-activity (readiness-potential) – the unconscious initiation of a freely voluntary act. *Brain* 106, 623–642
- Fried, I. *et al.* (2011) Internally generated preactivation of single neurons in human medial frontal cortex predicts volition. *Neuron* 69, 548–562
- Schurger, A. *et al.* (2012) An accumulator model for spontaneous neural activity prior to self-initiated movement. *Proc. Natl. Acad. Sci. U.S.A.* 109, E2904–E2913
- Murakami, M. *et al.* (2014) Neural antecedents of self-initiated actions in secondary motor cortex. *Nat. Neurosci.* 17, 1574–1582
- Jo, H-G. *et al.* (2013) Spontaneous EEG fluctuations determine the readiness potential: is preconscious brain activation a preparation process to move? *Exp. Brain Res.* 231, 495–500
- Böcker, K.B.E. *et al.* (2001) Stimulus-preceding negativity induced by fear: a manifestation of affective anticipation. *Int. J. Psychophysiol.* 43, 77–90
- Gluth, S. *et al.* (2013) Classic EEG motor potentials track the emergence of value-based decisions. *Neuroimage* 79, 394–403
- Miller, J. *et al.* (2010) Effects of clock monitoring on electroencephalographic activity. *Psychol. Sci.* 22, 103–109
- Haggard, P. and Eimer, M. (1999) On the relation between brain potentials and the awareness of voluntary movements. *Exp. Brain Res.* 126, 128–133
- Chen, R. *et al.* (1998) Time course of corticospinal excitability in reaction time and self-paced movements. *Ann. Neurol.* 44, 317–325
- Bengson, J.J. *et al.* (2014) Spontaneous neural fluctuations predict decisions to attend. *J. Cogn. Neurosci.* 26, 2578–2584
- Kagaya, K. and Takahata, M. (2011) Readiness discharge for spontaneous initiation of walking in crayfish. *J. Neurosci.* 30, 1348–1362
- Garcia-Perez, E. *et al.* (2007) Spontaneous electrical activity and behavior in the leech *Hirudo medicinalis*. *Front. Integr. Neurosci.* 1, 1–9
- He, B.J. *et al.* (2010) The temporal structures and functional significance of scale-free brain activity. *Neuron* 66, 353–369
- Silver, N. (2012) *The Signal and the Noise: The Art and Science of Prediction*, Penguin