


Guest Editorial: On the Possibility of a Unifying Framework for Serial Dependencies

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Serial effects in perception have been studied since the dawn of psychophysics. Color aftereffects greatly advanced the understanding of color vision in the 19th century, and motion aftereffects have intrigued perceptual scientists for centuries. Recent discoveries in visual attention and psychophysics have intensified interest in such effects. The current consensus is that they are not curiosities but serve an important function and can be critical for understanding perception.

In December 2015, a small group of vision scientists gathered for a 2-day workshop in Pisa to discuss these issues. The meeting (Serial Effects in Perception: Prediction, Priming, and Adaptation, December 11–12, 2014: www.pisavisionlab.org/sfx2014) brought together experts in varied types of serial effects: perceptual continuity, serial effects, priming, and adaptation. The abstracts of the meeting follow this introduction.

The aim was to discuss the various findings in an attempt to find common features as well as distinguishing traits. In the first session, on perceptual serial dependencies, David Whitney presented evidence that both lower and higher level perceptual mechanisms utilize assimilative trial to trial information: Current perceptions are biased toward previous ones (Fischer & Whitney, 2014; Liberman, Fischer et al., 2014). Whitney also introduced the concept of a “continuity field”: A zone in space and time where the brain looks for continuities. Although the extent of the continuity field might depend on the particular technique used for stimulus presentation and response, the concept seems useful to describe the benefits of serial effects: Things rarely change rapidly in the world so it might be beneficial to draw upon several snapshots overtime to represent the environment.

Cicchini and Burr tackled a complementary issue. According to their work, a simple formula determines the optimal weight of current and past information: If two stimuli are similar, it is beneficial to give a consistent weight to past information and this reduces noise; however, if two stimuli are markedly different, the weight of the past information should be very small. In this way, one obtains an optimal mechanism that discounts sensory fluctuations, yet is responsive to abrupt changes (Burr & Cicchini, 2014). Such an adaptive

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filter, akin to a Kalman filter, fits well with several findings on serial dependencies and this strategy may be incorporated in biological systems (Cicchini, Anobile, et al., 2014). Cicchini et al. showed how this model predicts nonlinearities in number-to-line mappings, previously thought to reflect logarithmic encoding (Dehaene, Izard, et al., 2008), and also provided new evidence that positive serial dependencies can occur at a strictly perceptual level even with diverse intervening responses.

The aim of the second session was to provide a picture of the current understanding of the brain as a mechanism for hypothesis-generation (aka prediction). Lars Muckli presented recent work showing that the brain automatically perceives stimulus change and extrapolates possible future stimulus features. Muckli used two-frame apparent motion finding that the brain is capable of both filling in missing frames as well as extrapolating the object trajectory (Muckli, Kohler, et al., 2005; Weigelt, Kourtzi, et al., 2007). Interestingly, his research also reveals considerable crosstalk between areas dedicated to motion perception and areas involved in motion prediction providing a strong argument that prediction is a critical brain function occurring even at the first stages of processing (Alink, Schwiedrzik, et al., 2010; Kaas, Weigelt, et al., 2010; Muckli, Kohler, et al., 2005; Weigelt, Kourtzi, et al., 2007; Wibrals, Bledowski, et al., 2009).

Floris de Lange followed up on this, discussing neurophysiological correlates of predictive coding. Predictive coding proposes that perception is the result of two separate processes that complement one another: predictions based on the current state of environment and mismatches between predictions and sensory signals (Friston, 2010; Rao & Ballard, 1999). Spatial and temporal context are known to play a major role in visual perception (Oliva & Torralba, 2007), but the precise mechanisms by which context and expectations modify the neural codes are still poorly understood. de Lange demonstrated that knowing the features of a stimulus in advance changes neuronal responses even as early as in V1 (Kok & de Lange, 2014; Kok, Brouwer, et al., 2013). Interestingly, repeated presentation of a stimulus produces weaker responses, consistent with well-known findings of neural repetition suppression with repeated search displays (Bichot & Schall, 1999; Kristjansson, Vuilleumier, et al., 2007); yet, the information content after repetition increases, consistent with the idea that serial presentation leads to optimization of perceptual processing.

Aldo Genovesio discussed the effects of stimuli and task on previous trials on prefrontal cortical activity in monkeys. His data are particularly revealing in that even when not explicitly required by task, past trial information is stored in a subset of prefrontal neurons (Genovesio, Brasted, et al., 2005; Genovesio, Brasted, et al., 2006; Genovesio, Tsujimoto, et al., 2006; Genovesio, Tsujimoto, et al., 2012; Tsujimoto, Genovesio, et al., 2012). Genovesio hypothesized that this information is crucial for the monkey's ability to understand and monitor its own actions and is, therefore, critical for learning and reward (Genovesio & Ferraina, 2014). Overall, this suggests that remembering the task is an automatic process that is nevertheless an active and important part of human cognitive abilities.

The second day of the conference started with a session on adaptation. Adaptation attracts interest not only because it is an intriguing form of plasticity and flexibility of brain circuits but also because it has proven an invaluable tool in psychophysics to watermark visual mechanisms and test their specificity (Thompson & Burr, 2009). There are, nevertheless many intriguing open questions, even paradoxes, regarding adaptation. Is adaptation beneficial? And, if so, why is it often accompanied by reduced neural activity?

In the first talk of the second day, Solomon argued that even seemingly simple brain circuits which exhibit surround inhibition, can, when adapted, display a host of behaviors depending on the specific experimental procedure and question (Solomon & Kohn, 2014).

However, Solomon warned about inferring functional principles from neural activity unless all details are taken into account. Also, a clear conclusion from Solomon's talk was that serial effects may come in many guises even though they obey a few simple principles.

Peter Foldiak discussed decorrelation and Anti-Hebbian adaptation. The main thrust of this work is that if two sensory signals are similar because of mutual correlation (such as when the two signals monitor similar parts of the visual field or when they are corrupted by the same noise source), it may be beneficial to decorrelate them by subtracting one from the other, increasing discriminability among the two signals. On a face value, this classic work may seem at odds with the approach of Kalman filtering which suggests that the benefit lies in averaging rather than subtracting stimuli. However, there are quite a few differences between the approaches; for instance, in Foldiak's work the goal of the system is to discriminate the various signals, whereas in Kalman filtering the goal is to have representations close to veridical. Also, another crucial issue is the nature of noise. In the standard version of the Kalman filter, noise is assumed independent, whereas in the decorrelation framework, it is assumed that the same noisy information sneaks into both signals (de Gardelle & Summerfield, 2011). Indeed, a final framework for assessing which mechanism is optimal needs to take into account several details and the answer, likely will vary accordingly.

Peter Thompson closed the session, describing an example of cross-modal adaptation, which he cleverly used as a tool to demonstrate multimodal representations in the brain. Such cross-modal adaptation effects are extremely interesting, as they have notable implications for understanding the mechanisms involved in adaptation and the level at which they occur.

One of the themes of the workshop was to bridge gaps between disciplines. While the interest in sequential dependencies in basic vision science is in many cases recent, a large literature spanning over 20 years has emerged within the field of visual attention, showing how recent attention deployments strongly influence future ones.

Typically, attentional priming shows how response times are speeded (Maljkovic & Nakayama, 1994) or accuracy increased (Asgeirsson, Kristjansson, et al., 2014) if attentional priorities remain constant between trials. Priming can have a dominating influence on attentional functioning (for review, Kristjansson & Campana, 2010; Kristjansson, Heimisson, et al., 2013), but while priming is often merely thought of as a facilitation of reaction times, having little relevance to perception, Arni Kristjansson was able to show that under the appropriate circumstances priming affects attentional choice (Brascamp, Pels, et al., 2011), overcomes masking (Asgeirsson & Kristjansson, 2011; Sigurdardottir, Kristjansson, et al., 2008), and releases items from crowding (Kristjansson, Heimisson, et al., 2013), which has strong implications for perception.

Gianluca Campana attempted to pin down the neural substrates of priming and to what extent areas involved in motion extrapolation share resources with those for perception. Campana showed that motion extrapolation in adapted regions of the visual field is affected consistently (Battaglini, Campana, et al., 2015). Along the same lines, he showed that if motion perception is primed (by exposure to a moving patch), time to contact estimation is affected. Overall, these results support a strong entwinement between mechanisms for perception, prediction, and extrapolation, which may connect priming to mechanisms of prediction (Kanai & Verstraten, 2005).

Lastly, Mamassian made the case for multiple scales of adaptation in the brain. Chopin and Mamassian (2012) analyzed effects of recent or remote stimuli on the perception of an oriented grating and found that while recent stimuli have a repulsive effect, more distant trials in time exert a positive aftereffect on perception. Mamassian presented evidence that the strongest repulsive aftereffects occur at the beginning of a series of stimuli with similar

intensity (McDermott, Chopin, et al., 2015). Interestingly, there were both biases in perceived motion direction (adaptation) in addition to a reduction in discrimination threshold, reflecting perceptual learning. The two may not necessarily occur on the same timescales, however.

The last session of the workshop dealt with how we build averages of the perceptual input and infer the statistics and rules of novel environments or settings.

József Fiser presented evidence that the brain employs Bayesian principles in learning which nicely complemented Maloney's presentation (see below) and extended the Bayesian algorithms (that take reliability into account) to the purposeful learning of cognitive associations. Second, Fiser examined what determines intertrial dependencies, by manipulating stimulus sequences so that the sequence itself was predictable for the observer. In this way, Fiser demonstrated that under some circumstances observers can incorporate the precise structure of the sequence to perform better. Simultaneously, however, observers display regression toward the mean and short-term intertrial serial effects.

Geoff Boynton presented work where a train of stimuli that varied on several features (size, spatial frequency, position) was presented and observers had to reproduce the average stimulus. While, for several dimensions, a recency effect was seen (the latest stimuli contributing most to the average), positional judgments displayed a primacy effect with the first one or two stimuli dictating the average (Hubert-Wallander and Boynton, 2015). These data present a challenge for the idea that a single unifying concept may account for all serial effects.

Lastly, Larry Maloney investigated the time course of learning a new set of motor rules, what determines learning, and whether the rules can be stored and retrieved as necessary. In his experiment, people reached to a target and estimated their chances of success. Without warning, participants' elbows were restrained so that reaching movements could only be performed by moving the trunk. Subjects again gained a new appropriate motor behavior. Observers' behavior could be modeled successfully with Bayesian updating, a strategy which weights information by its novelty and reliability, akin to the Kalman filter invoked by Burr and Cicchini (2014). In essence, it seems that reliability-based updating might occur at different scales of processing in the brain.

Overall, this gathering of researchers from differing subdisciplines was inspiring. Clearly, history effects are ubiquitous in perception, seen in many paradigms that probably reflect a number of differing mechanisms. As for the question of finding a unifying framework for serial effects, there are clear obstacles to that. The diversity of paradigms employed and limited knowledge of several, potentially important variables suggest that the task will be difficult.

Nevertheless, several considerations may indicate that the varied results might become part of a larger, framework that explains how the past is used to predict the present:

- (1) Natural statistics contain strong serial correlations as the world tends to be stable from moment to moment. So, whether it is a window spanning several seconds as Whitney suggests, or a flexible self-adjusting mechanism as Burr and Cicchini propose, it is highly likely that the brain has developed strategies to exploit such regularities. Indeed, in some perceptual domains such as motion integration or transaccadic perception, the brain displays a remarkable ability to integrate information over large time intervals (Burr & Morrone, 1996; Burr & Santoro, 2001; Cicchini, Binda, et al., 2013; Neri, Morrone, et al., 1998; Panichi, Burr, et al., 2012).
- (2) Although the human brain is remarkably flexible, we often engage in continuous or sustained tasks that would benefit from fine tuning of responses rather than flexibility

(Kristjansson & Campana, 2010). It may be beneficial to keep track of what we have been doing before instead of starting afresh. This feature should not be underestimated as it might be critical in many task of fine skills and might even enable learning itself, as Genovesio suggests (Genovesio & Ferraina, 2014).

- (3) The brain is capable of decoding long chunks of information overtime, such as scenes or movies. It possesses the ability to elaborate and recognize information spread overtime. In normal perception what are these mechanisms up to? Are they inactive or do they play a strong role and enable predictions?

All this highlights that a common framework for serial dependencies might be feasible. A central governing principle might involve the benefits of taking the past into account while interpreting the present environment. (Busse, Ayaz, et al., 2011; Frund, Wichmann, et al., 2014).

It is easy to envision teleological reasons behind serial effects while science demands empirical demonstrations. The findings presented at the meeting hopefully serve this goal and bring to mind the idea of living organisms living in a 4D world where temporal information and context is as important and informative as spatial context.

What is needed for a firmer grounding for this framework? Clearly, it would be of help to see whether serial dependencies vary consistently with the amount of available information or whether they reflect fixed mechanisms operating on precise timescales. Possibly one of the most urgent tasks is to demonstrate up to which point serial dependencies comply with rules of optimal integration and bring about a real decrease of stimulus uncertainty.

At the same time, it is crucial to understand why priming is sometimes positive and sometimes negative (Kanai & Verstraten, 2005). Possibly, the recent finding that negative priming is retinotopic and positive priming is spatiotopic may help in this (Yoshimoto, Uchida-Ota, et al., 2014). This is an oddity that cannot be dismissed by simply saying that the brain tracks temporal correlations in natural scenes.

The results that were, perhaps, the most surprising were Boynton's. Why, all other things being equal, do we set our minds with the first stimuli while for other tasks we draw on our recent past. How could the continuity field approach, or even a Bayesian framework, accommodate these results? A possible explanation is that repetition effects operate on varied timescales (see e.g., Brascamp, Pels, & Kristjansson, 2011) and reflect the operation of diverse neural mechanisms, but firmer evidence is needed to clinch such an argument.

If a unitary framework for serial dependencies in vision is to emerge, it will surely take time. Yet, the participants of the workshop were in agreement that such meetings help in constructing bridges between fields of research, which is crucial for any such progress.

References

- Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W., & Muckli, L. (2010). Stimulus predictability reduces responses in primary visual cortex. *Journal of Neuroscience*, *30*, 2960–2966.
- Asgeirsson, A. G., & Kristjansson, A. (2011). Episodic retrieval and feature facilitation in intertrial priming of visual search. *Attention, Perception, & Psychophysics*, *73*, 1350–1360.
- Asgeirsson, A. G., & Kristjansson, A., et al. (2014). Independent priming of location and color in identification of briefly presented letters. *Attention, Perception, & Psychophysics*, *76*, 40–48.
- Battaglini, L., & Campana, G., et al. (2015). Probing the involvement of the earliest levels of cortical processing in motion extrapolation with rapid forms of visual motion priming and adaptation. *Attention, Perception, & Psychophysics*, *77*, 603–612.

- Bichot, N. P., & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience*, *2*, 549–554.
- Brascamp, J. W., Pels, E., & Kristjansson, A. (2011). Priming of pop-out on multiple time scales during visual search. *Vision Research*, *51*, 1972–1978.
- Burr, D., & Cicchini, G. M. (2014). Vision: Efficient adaptive coding. *Current Biology*, *24*, R1096–R1098.
- Burr, D. C., & Morrone, M. C. (1996). Temporal impulse response functions for luminance and colour during saccades. *Vision Research*, *36*, 2069–2078.
- Burr, D. C., & Santoro, L. (2001). Temporal integration of optic flow, measured by contrast and coherence thresholds. *Vision Research*, *41*, 1891–1899.
- Busse, L., & Ayaz, A., et al. (2011). The detection of visual contrast in the behaving mouse. *The Journal of Neuroscience*, *31*, 11351–11361.
- Chopin, A., & Mamassian, P. (2012). Predictive properties of visual adaptation. *Curr Biol*, *22*, 622–626.
- Cicchini, G. M., & Anobile, G., et al. (2014). Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 7867–7872.
- Cicchini, G. M., & Binda, P., et al. (2013). Transient spatiotopic integration across saccadic eye movements mediates visual stability. *Journal of Neurophysiology*, *109*, 1117–1125.
- de Gardelle, V., & Summerfield, C. (2011). Robust averaging during perceptual judgment. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 13341–13346.
- Dehaene, S., & Izard, V., et al. (2008). Log or linear? Distinct intuitions of the number scale in Western and Amazonian indigene cultures. *Science*, *320*, 1217–1220.
- Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience*, *17*, 738–743.
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews. Neuroscience*, *11*, 127–138.
- Frund, I., & Wichmann, F. A., et al. (2014). Quantifying the effect of intertrial dependence on perceptual decisions. *Journal of Vision*, *14*, 1–16.
- Genovesio, A., & Brasted, P. J., et al. (2005). Prefrontal cortex activity related to abstract response strategies. *Neuron*, *47*, 307–320.
- Genovesio, A., & Brasted, P. J., et al. (2006). Representation of future and previous spatial goals by separate neural populations in prefrontal cortex. *The Journal of Neuroscience*, *26*, 7305–7316.
- Genovesio, A., & Ferraina, S. (2014). The influence of recent decisions on future goal selection. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *369*, 20130477.
- Genovesio, A., & Tsujimoto, S., et al. (2006). Neuronal activity related to elapsed time in prefrontal cortex. *Journal of Neurophysiology*, *95*, 3281–3285.
- Genovesio, A., & Tsujimoto, S., et al. (2012). Encoding goals but not abstract magnitude in the primate prefrontal cortex. *Neuron*, *74*, 656–662.
- Hubert-Wallander, B., & Boynton, G. M. (2015). Not all summary statistics are made equal: Evidence from extracting summaries across time. *Journal of Vision*, *15*, 5.
- Kaas, A., & Weigelt, S., et al. (2010). Imagery of a moving object: The role of occipital cortex and human MT/V5+. *Neuroimage*, *49*, 794–804.
- Kanai, R., & Verstraten, F. A. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research*, *45*, 3109–3116.
- Kok, P., & Brouwer, G. J., et al. (2013). Prior expectations bias sensory representations in visual cortex. *Journal of Neuroscience*, *33*, 16275–16284.
- Kok, P., & de Lange, F. P. (2014). Shape perception simultaneously up- and downregulates neural activity in the primary visual cortex. *Current Biology*, *24*, 1531–1535.
- Kristjansson, A., & Campana, G. (2010). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention, Perception, & Psychophysics*, *72*, 5–18.
- Kristjansson, A., & Heimisson, P. R., et al. (2013). Attentional priming releases crowding. *Attention, Perception, & Psychophysics*, *75*, 1323–1329.

- Kristjansson, A., & Vuilleumier, P., et al. (2007). Neural basis for priming of pop-out during visual search revealed with fMRI. *Cerebral Cortex*, *17*, 1612–1624.
- Liberman, A., & Fischer, J., et al. (2014). Serial dependence in the perception of faces. *Current Biology*, *24*, 2569–2574.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, *22*, 657–672.
- McDermott, K., Chopin, A., et al. (2015). History effects in perception after manipulating the statistics of the environment. Vision Science Society 15th Annual Meeting, St. Pete Beach, Florida, USA.
- Muckli, L., & Kohler, A., et al. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biology*, *3*, e265.
- Neri, P., & Morrone, M. C., et al. (1998). Seeing biological motion. *Nature*, *395*, 894–896.
- Oliva, A., & Torralba, A. (2007). The role of context in object recognition. *Trends in Cognitive Sciences*, *11*, 520–527.
- Panichi, M., & Burr, D., et al. (2012). Spatiotemporal dynamics of perisaccadic remapping in humans revealed by classification images. *Journal of Vision*, *12*, 11.
- Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*, 79–87.
- Sigurdardottir, H. M., & Kristjansson, A., et al. (2008). Repetition streaks increase perceptual sensitivity in visual search of brief displays. *Visual Cognition*, *16*, 643–658.
- Solomon, S. G., & Kohn, A. (2014). Moving sensory adaptation beyond suppressive effects in single neurons. *Current Biology*, *24*, R1012–1022.
- Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, *19*, R11–R114.
- Tsujimoto, S., Genovesio, A., & Wise, S. P. (2012). Neuronal activity during a cued strategy task: Comparison of dorsolateral, orbital, and polar prefrontal cortex. *Journal of Neuroscience*, *32*, 11017–11031.
- Weigelt, S., & Kourtzi, Z., et al. (2007). The cortical representation of objects rotating in depth. *Journal of Neuroscience*, *27*, 3864–3874.
- Wibral, M., & Bledowski, C., et al. (2009). The timing of feedback to early visual cortex in the perception of long-range apparent motion. *Cerebral Cortex*, *19*, 1567–1582.
- Yoshimoto, S., & Uchida-Ota, M., et al. (2014). Effect of light level on the reference frames of visual motion processing. *Journal of Vision*, *14*, 6.

Serial Effects in Perception: Prediction, Priming, and Adaptation, Pisa, December 11-12 2014

Abstracts

The Continuity Field: A Mechanism for Perceptual Stability via Serial Dependence

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Abstract

A critical function of vision is to maintain stable perception of objects so they look the same from moment to moment. This is a challenge because visual input is noisy and discontinuous due to, for example, shadows, motion, occlusion, changes in lighting, noise, and so forth. Although a classic question, the mechanism that links the perception of an object's identity and properties from moment to moment is unknown. Here, we demonstrate the perceptual constancy field, a novel mechanism of object constancy built on serial dependence. We found that on a given trial, a subject's perception of the orientation of a grating reflected not only the currently viewed stimulus but also a systematic attraction toward the orientations of the previously viewed stimuli. We found the same serial dependence in the perception of facial expression. This perceptual attraction extended over several trials and seconds and displayed clear tuning to the difference (in orientation or facial expression) between the sequential stimuli. Furthermore, serial dependence in object perception was spatially specific and selective to the attended object within a scene. Several control experiments showed that the perceptual serial dependence that we report cannot be explained by effects of priming, known hysteresis effects, visual short-term memory, or expectation. Instead, there is a systematic influence of recent visual experiences on perception at any given moment: Visual percepts, even of unambiguous stimuli, are attracted toward what was previously seen. Our results reveal a novel mechanism—the Continuity Field—that helps maintain stable object and scene representations in the face of a dynamic and noisy environment.

1.2 Serial Dependencies Cause Logarithmic-Like Compression of the Numberline

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Abstract

Mapping of number onto space is fundamental to measurement and mathematics. However, numberline mapping of young children, unschooled adults, and adults under attentional load or making speeded responses shows strong compressive nonlinearities, thought to reflect intrinsic logarithmic mechanisms, later “linearized” by education. Here, we advance and test an alternative explanation: that the nonlinearity results from adaptive mechanisms incorporating the statistics of recent stimuli. This theory predicts strong serial dependencies, whereas a static logarithmic nonlinearity predicts trial-wise independence. We found strong and highly significant correlations between numberline mapping of the current trial and the magnitude of the previous trial, in both adults and school children. The dependencies were particularly strong at the beginning of pointing trajectories (Dotan & Dehaene, 2014). The current response was influenced by up to 20% by the previous trial value is sufficient to account quantitatively for the compressive shape of the numberline. A Bayesian-like model shows that the dynamic serial dependency leads to a reduction of reproduction error and hence improvement in overall accuracy.

Reference

Dotan, D., & Dehaene, S. (2014). How do we convert a number into a finger trajectory? *Cognition*, *129*, 512–529.

2.1 Cortical Predictions During Motion Illusions**Lars Muckli**

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Abstract

We have used a variety of motion illusions to investigate serial dependency processing in our cortical visual system measured with functional brain imaging. Using two-dimensional long-range apparent motion, three dimensional rotational apparent motion, and complex scene motion, we found that different stages of cortical processing fill-in intermediate object positions and extrapolate to upcoming predicted visual scenes (Alink, Schwiedrzik, Kohler et al., 2010; Maus, Weigelt, Nijhawan, et al., 2010; Vetter, Edwards, & Muckli, 2012; Vetter, Grosbras, & Muckli, 2013; Weigelt, Kourtzi, Kohler, et al., 2007). The cortical visual system extrapolates intermediate stimulation positions and broadcasts this expectation across different hierarchical processing stages. Motion extrapolations rely only on conscious illusion perception when the temporal integration becomes longer (Vetter et al., 2014). Thus, serial dependency is tracked by the visual system with and without conscious perception of motion. The findings illustrate how the visual system works in synergy across different processing stages to anticipate upcoming visual stimulation.

References

Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W., & Muckli, L. (2010). Stimulus predictability reduces responses in primary visual cortex. *Journal of Neuroscience*, *30*, 2960–2966.

- Maus, G. W., Weigelt, S., Nijhawan, R., & Muckli, L. (2010). Does area V3A predict positions of moving objects? *Frontiers in Psychology, 1*, 186.
- Vetter, P., Edwards, G., & Muckli, L. (2012). Transfer of predictive signals across saccades. *Frontiers in Psychology, 8*, 176.
- Vetter, P., Grosbras, M. H., & Muckli, L. (2013). TMS over V5 disrupts motion prediction. *Cerebral Cortex*.
- Vetter, P., Sanders, L. L. O., & Muckli, L. (2014). Dissociation of prediction from conscious perception. *Perception, 43*, 1107–1113.
- Weigelt, S., Kourtzi, Z., Kohler, A., Singer, W., & Muckli, L. (2007). The cortical representation of objects rotating in depth. *Journal of Neuroscience, 27*, 3864–3874.

2.2 How Do Prior Expectations Change Sensory Processing?

Floris de Lange

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Abstract

Although there is ample behavioral evidence for the predictive nature of perception, the incorporation of prior expectations in the neural computations underlying perception is still poorly understood.

In my lecture, I will review recent work on how prior expectations about the sensory world change the neural computations that give rise to perception. I will highlight recent neuroimaging data (Magnetoencephalography [MEG] and functional Magnetic Resonance Imaging [fMRI]) and methods (multivariate classification techniques) that show how stimulus expectations modify the sensory response. I will also contrast the effects of prior expectation with the modulatory effects of selective attention and adaptation.

In the spirit of the workshop, I will also focus on new data and ideas that we are currently testing with respect to serial effects in perception.

2.3 Influence of Trial History on Prefrontal Cortex Activity in the Macaque Monkeys

Aldo Genovesio

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Abstract

Monitoring the trial history in terms of the animal's previous choices can be important not only when required by the task but also when irrelevant to the task. We started to study the dorsolateral prefrontal cortex representation of the past spatial goals adopting a strategy task in which maintaining previous goal information across trials was a task requirement (Genovesio, Brasted, & Wise, 2006). This task required the monkeys to stay or shift from the previous response when the stimulus presented in a given trial was either the same or different, respectively. We identified separate populations of neurons encoding past and future goals. One function underneath this separation could be to allow an efficient output motoring function directed to establish whether a previously planned goal was accomplished or still pending. This result is in contrast with the

absence of trial history modulation of other prefrontal areas such as the orbitofrontal cortex and the frontal pole cortex (Tsujimoto, Genovesio, & Wise, 2012). In a more recent study (Genovesio, Tsujimoto, Navarra, et al., 2014), we tested whether the prefrontal cortex's neurons were modulated by the trial history even when not relevant to the task. We studied the activity of dorsolateral and periarculate neurons in a distance discrimination task in which the monkeys were required to discriminate the distance from screen center of two stimuli, one blue circle and one red square, presented sequentially, by choosing the stimulus farther from screen center when the two stimuli appeared together to the right and to the left of center. We found that neurons represented the previous goal location and its color but not others equally not relevant information such as the distance and the color of the stimuli presented in the previous trials (Genovesio et al., 2014). This result indicates that the monitoring function of the dorsolateral prefrontal cortex although goes beyond task relevance remains, however, restricted to goal information. Previous goal information is likely to be maintained in memory for many purposes such as exploring new alternatives in the exploration or exploitation tradeoff or for finding new problem-solving strategies (Genovesio & Ferraina, 2014).

References

- Genovesio, A., Brasted, P. J., & Wise, S. P. (2006). Representation of future and previous spatial goals by separate neural populations in prefrontal cortex. *Journal of Neuroscience*, *26*, 7305–7316. doi:10.1523/JNEUROSCI.0699-06.2006
- Genovesio, A., & Ferraina, S. (2014). The influence of recent decisions on future goal selection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*, 20130477. doi:10.1098/rstb.2013.0477
- Genovesio, A., Tsujimoto, S., Navarra, G., Falcone, R., & Wise, S. P. (2014). Autonomous encoding of irrelevant goals and outcomes by prefrontal cortex neurons. *Journal of Neuroscience*, *34*, 1970–1978. doi:10.1523/JNEUROSCI.3228-13.2014
- Tsujimoto, S., Genovesio, A., & Wise, S. P. (2012). Neuronal activity during a cued strategy task: Comparison of dorsolateral, orbital, and polar prefrontal cortex. *The Journal of Neuroscience*, *32*, 11017–11031. doi:10.1523/JNEUROSCI.1230-12.2012.

3.1 Adaptation in the Context of Normalization

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Abstract

How an object is perceived depends on the temporal context in which it is encountered. Sensory signals in the brain also depend on temporal context, a phenomenon often referred to as adaptation. Traditional descriptions of adaptation effects emphasize various forms of response fatigue in single neurons, which grow in strength with exposure to a stimulus. Recent work on vision, and other sensory modalities, has shown that this description has substantial shortcomings. Here, we review our emerging understanding of how adaptation alters the balance between excitatory and suppressive signals, how effects depend on adaptation duration, and how adaptation influences representations that are distributed within and across multiple brain

structures. This work points to a sophisticated set of mechanisms for adjusting to recent sensory experience and suggests new avenues for understanding their function.

3.2 Anti-Hebbian Decorrelation as a Model of Sensory Adaptation

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Abstract

The anti-Hebbian hypothesis states that the strengthening of inhibition or the weakening of excitation between correlated neurons or channels is a functionally important mechanism for the formation of neural connections necessary for the formation of sensory representations. Sensory adaptation and aftereffects can be seen as a side effect of this general mechanism. I will review a range of relevant neurophysiological, psychophysical, and computational results that have emerged since this hypothesis has been first proposed.

3.3 Cross-Modal Transfer of the Tilt-Aftereffect From Vision to Touch

Peter Thompson and Dafni Krystallidou

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Abstract

There is increasing evidence that some aftereffects can be transferred from one modality to another. Following the demonstration by Konkle, Wang, Hayward, and Moore (2009) that visual motion adaptation can produce a tactile motion aftereffect, we have conducted a series of experiments investigating whether visual adaptation to orientation can also affect our sense of touch. In each experiment a pair of points, separated by 30 mm, was touched on the subject's forehead, the task being to determine whether an imaginary line between the points tilted clockwise or anticlockwise from vertical. In Experiment 1, subjects were adapted to visually presented tilted gratings (15°) and the effect on two-point orientation discrimination determined. Results ($n = 13$) indicate that visual tilt adaptation produces a shift in the perceived tactile tilt in an analogous fashion to the visual tilt aftereffect. The magnitude of the effect was approximately 2.5° . In Experiment 2, we investigated the reference frame of the aftereffect. Subjects repeated Experiment 1 but with their heads tilted during the adaptation phase by 15° so that the gratings were aligned with the vertical meridian of the retina. The resulting tactile aftereffect ($n = 14$) was approximately 2.6° , similar to the effect in Experiment 1. This suggests that the effect is determined by a gravitational rather than a purely visual frame of reference. We are currently examining a condition in which subjects adapt to a vertical grating with heads tilted at 15° . This adaptation is known to produce a visual tilt aftereffect; however, if the effect described here is gravitationally based, this adaptation should produce no tactile illusion.

Reference

Konkle, T., Wang, Q., Hayward, V., & Moore, C. I. (2009). Motion aftereffects transfer between touch and vision. *Current Biology*, *19*, 745–750.

4.1 How Attention Priming Dominates Perception: Influences on Attentional Choice, Crowding, Masking and Liking of Stimuli

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Abstract

Priming of attention has often been studied as if it is a curiosity in visual search. I propose that its' dominating influence on perception yields fundamental insights into perceptual processing, revealing how the visual system manages to keep the visual world stable and update key representations quickly and efficiently. I will describe recent results from four rather different experimental approaches that highlight the strong influence that attention priming plays in various aspects. These studies show that attentional priming has a strong effect on various measures apart from its influence on visual search: (a) Priming almost completely determines free choice between two different stimuli; (b) Priming can release items from visual crowding; (c) Priming can aid recovery from masking effects; (d) Priming influences the evaluation of stimuli, in other words how much they are liked. All these results show how the visual system strongly prefers items that were previously attended, and more broadly showing how the past determines the present in visual perception.

4.2 Rapid Priming and Adaptation Modulate Prediction-of-Motion: Implications for the Involved Levels of Processing

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Abstract

Prediction-of-Motion can be investigated with a time-to-contact (TTC) estimation of a target passing behind an occluder. Previous findings have shown that TTC estimation can be modulated by motion adaptation of the occluded area, suggesting that the mechanism underlying Prediction-of-Motion could be a perceptual one. Here, we exploited rapid forms of visual motion priming and adaptation that were shown to occur at the earliest levels of visual cortical processing. In particular, while TMS studies found an involvement of early and intermediate visual areas along the cortical hierarchy in the rapid motion aftereffect, psychophysical studies found that rapid visual motion priming could not be elicited by stimuli (such as complex motion) processed by intermediate or higher level visual areas. By using different exposure times of directional motion (the same producing either rapid visual motion priming or rapid motion aftereffect) presented in the occluder area just before the target disappeared behind it, we found that longer (yet sub-second) exposures to motion in the same direction of the target increased TTC estimates, whereas shorter exposures decreased TTC estimates. These results indicate that rapid forms of motion adaptation and motion priming modulate extrapolated motion. Thus, motion extrapolation might occur at the first levels of cortical motion processing, where these rapid mechanisms take place.

4.3 Visual Adaptation to Changes in Statistical Properties of the Environment

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Abstract

Repeated stimulus presentations can lead to dramatic changes in the perception of subsequent stimuli. Two such phenomena are biased perception (aftereffects) due to adaptation and increased sensitivity due to perceptual learning. Here, we study the interaction of these two phenomena.

Observers were asked to indicate whether the direction of motion of a briefly presented field of random dots was to the left or right of a cued direction. Stimuli were presented by method of constant stimuli with directions of motion chosen from a nonuniform distribution designed to induce a bias. This was achieved by manipulating the frequency with which different directions of motion were presented: For both the left and right halves of the stimulus distribution, the left end of the range was shown few times and the right end of the range was shown many times. Observers trained on this task for an hour a day for five consecutive days.

The data demonstrate both a bias in perceived direction of motion due to adaptation and a reduction in discrimination threshold due to learning. Both phenomena asymptotically approach some maximum magnitude both within and across days with some of the effects carrying over from one day to the next. These results are consistent with a model based on a process where stimuli induce slight changes in the tuning of neural populations coding for motion direction. Such alterations of these tuning functions are in line with physiological measurements and similar models have been used to explain various phenomena associated with long-term exposure to the image statistics of natural scenes.

5.1 Integrating Visual Information Overtime

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Abstract

Perceptual decisions often require integration of information across time. Even a static scene is effectively sampled overtime via saccades. We are interested in how humans combine serially presented information into overall judgments of simple visual stimuli.

For the first experiment, subjects viewed a sequence of 10 discs presented sequentially varying in both spatial position and size. Subjects were precued on each trial to indicate either the perceived center or the mean size of the discs. A set of 10 weights was obtained for each subject that reflects the relative influence that discs in each temporal interval had on the overall judgment of position or size.

For estimating the central location, subjects show a much stronger weight for early discs—a “primacy” effect. For mean size, however, subjects showed stronger weighting for discs presented later in the sequence—a “recency” effect.

In subsequent experiments, subjects were asked to indicate the mean direction of motion of a sequence of coherently moving dots and the mean facial expression of a sequence of faces ranging from happy to sad. Both of these experiments showed a recency effect, with the latest directions of motion and facial expressions contributing much more weight than earlier stimuli.

Together, these experiments show that the way subjects integrate information across time to make a decision about central tendency depends on the stimulus domain. We discuss two explanations for this. First, it may be that these differences reflect different neural mechanisms involved with bottom-up mechanisms that integrate information overtime. Second, these differences may reflect different high-level processes that have different decision-making constraints. For example, it may be optimal to make early, rapid decisions about mean spatial location in order to make quick eye movements to the perceived center. Decisions about other stimulus domains like facial expression might be optimally made by emphasizing later information that better reflect the current state of a changing stimulus.

5.2 Factors That Influence Judging and Guessing About Probabilistic Event Sequences

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Abstract

Previous studies have reported several factors, including prior knowledge, past experience, immediately preceding events, and rate of event repetitions that influence humans' ability to predict and perceive sequentially occurring probabilistic events. However, many of these factors are correlated and most earlier studies made little effort to disentangle their confounding effects. I will present a series of human behavioral experiments, in which we systematically inspected the separate and joint effects of these factors within a simple visual perceptual paradigm. We found that, rather than simply balancing past and present statistics, the best model describing human performance is probabilistic and it assumes a parallel working of several factors: (a) reliance on prior statistical knowledge of the sequence as a function of stimulus uncertainty, (b) a "regression to the mean" kind of effect that could reflect a general strategy of noncommitment, and (c) an independent short-term repetition effect which influences performance asymmetrically.

5.3 You Know You Can't Do That: Effects of Experience and Abruptly Imposed Movement Constraints on Sequential Estimation of Success Probability

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Abstract

In typical sequential judgment tasks, the subject is told the probability of occurrence of one of two possible mutually exclusive outcomes in advance. In many everyday tasks, however, we must somehow estimate the probability of the various outcomes. One possible source of information is our actual success or failure in repeated trials. Another possibility is that we base our estimate in part on a model of how our body works. The evident advantage of the latter is that it can be much less painful than trial and error learning. The evident disadvantage is that reliance on incorrect models can lead to errors in estimating our own capabilities.

In two experiments, we examined human estimation of the probability of success in a repeated motor task. Subjects performed 100 speeded pointing trials on a horizontal touch screen. The

target was a bulls-eye with a small center circle and a larger surround. Before each trial, subjects estimated their probability of hitting the target and their probability of hitting the center circle. They then attempted to hit the target. After every trial they received feedback. We compared human performance to an ideal Bayesian updating model for the first 40 trials. Performance was consistent with Bayesian updating and the gradual accumulation of information in the form of a beta distribution prior.

However, without warning, during trials 41–70, we either fixed their elbow at 90° (Experiment 1) or constrained them to use their nondominant hand (Experiment 2). This intervention mimics the consequences of unexpected loss of motor function due to injury or stroke. At the 71st trial, we removed the constraint.

We found that—for many subjects—added constraints led to large and persistent underestimation of target-center hit rates even after normal movement was restored. Subjects based their estimates not only on their experience of success and failure but also on an incorrect model of how constraint would affect their performance.

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