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The Emergence of Stimulus-Response Associations from Neural Activation Fields: Dynamic Field Theory

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Abstract

Dynamic Field Theory is based on spatially continuous representations of parameter space and provides a mathematical framework to study the metric structure of representations. We review evidence for such metric structure and provide a Dynamic Field Theory of stimulus-response association to account for effects caused by the metric structure of representations such as the distance effect and the interaction of the Hick and Hyman effects with stimulus metrics. We show how the integration of different sources of information contributes to stimulus-response association by providing a new model of the manual Stroop effect.

Introduction

People continuously interact with their environment generating simple behaviors such as pointing or reaching, but also using more complex skills such as using a computer. Everyday life thus requires a highly flexible neural system that may adjust and readjust its behavior depending on situational constraints, may continuously learn new responses toward sensory inputs and may adapt already existing stimulus-response mappings. Cognitive scientists and psychologists have studied how neural systems learn to react to input from sensory surfaces and how they compute the corresponding output through stimulus-response association paradigms. If a participant is asked to respond to a red stimulus by pressing a right button and to a green stimulus by pressing a left button, this requires a stimulus-response mapping that the subject probably has never encountered before. Nevertheless, within a very few practice trials participants are able to perform such a task.

While such tasks might appear trivial to the participant, it is not obvious how the nervous system might achieve them. One way researchers have tried to study stimulus-response associations consists of bringing into conflict multiple sources of response specification. In the classic Stroop task (review by MacLeod, 1991), for instance, the meaning of color words is brought into conflict with the color the words are printed in. Participants have to speak out loud the latter and are slowed in their response if that color is incongruent with the meaning of the color word.

Neural accounts for such conflict in connectionist models are typically based on units that code for entire stimulus or response categories. For instance, neurons representing the print-color information "red" or the word

meaning information "red" may provide input to neurons encoding the oral response "red" (Cohen, Dunbar & McClelland, 1990; Roelofs, 2003; see Figure 1).

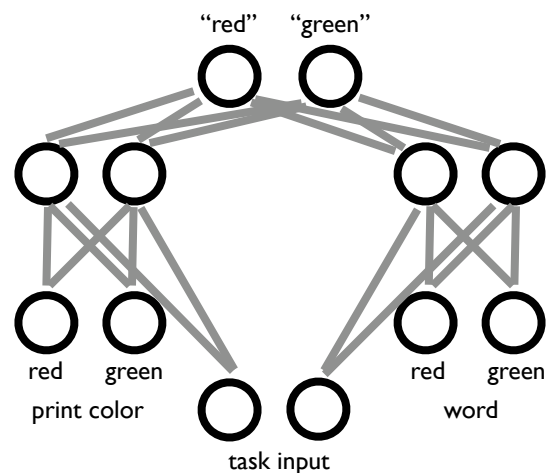


Figure 1: Connectionist model of the Stroop paradigm, redrawn after Cohen, Dunbar & McClelland (1990)

Neurophysiological evidence on the other hand suggests that features are represented in continuous feature maps, in which populations of neurons with broad tuning curves are activated. Across neocortex and other parts of the central nervous system, the location of neurons in the network determines what information neurons encode (space code principle). In many cortical areas, topographic mapping makes that neighboring neurons encode similar kinds of information. Independently of topography (anatomical coordinates), neuronal representations of parameters can be constructed by sorting neurons according to what they code (functional coordinates) (Georgopoulos et al., 1982). Neuronal interaction is sensitive to this metric structure of representations, meaning that neurons representing similar information excite each other while neurons representing dissimilar information inhibit each other. Wilson and Cowan (1973) as well as Amari (1977) have shown that the processing of information in such cortical and subcortical networks is mathematically well described by continuous dimensions with an associated metric defined by interaction.

How may stimulus-response associations occur within such continuous maps? Does the underlying metric structure of feature representations influence the way stimulus-response associations are realized?

Dynamic Field Theory (Kopecz & Schöner, 1995; Thelen et al., 2001; Erlhagen & Schöner, 2002) is an approach to the representation of stimulus and response parameters that takes their natural metric structure into account while also being consistent with basic neurophysiological principles (Amari, 1977). Within Dynamic Field Theory (DFT), task and stimulus parameters define the dimensions of a functional space, over which an activation field is defined. The activation field evolves continuously in time under the influence of inputs and brain-like interactions within the field. Inputs may derive from current sensory stimulation, but also from prior knowledge about possible choices, memory traces of prior activation or subthreshold cues. Localized peaks of activation represent perceptual or motor decisions as interaction is sufficiently strong to be capable of making detection decisions (Bicho, Mallet & Schöner, 2000) or selecting one out of a set of behavioral options (Kopecz & Schöner, 1995). Based on the notion of population distributions of activation (Erlhagen et al., 1999), Dynamic Field Theory is thus a process model of neuronal decision making.

Many perceptual decision making tasks require a discrete response, for instance, as a label, to graded sensory information. If the neuronal support for decisions is functionally continuous and metric in nature, how may categorical responses emerge from such representations? To categorically react to graded sensory information, prior information is required that represents properties of the categories. When prior activation has the appropriate metric and strength, Dynamic Fields respond in a categorical mode, in which the location of a localized peak of activation is determined by the location of the prior distribution of activation and the generation of the peak driven by a broad boost of activation while the current sensory input is weak (Wilimzig & Schöner, 2005). In contrast, the field continuously estimates current parameters, as required for sensorimotor decision making to support pointing or grasping movements, when the current stimulus input is the dominant contribution and prior activation provides a smaller contribution (Erlhagen & Schöner, 2002; see also Wilimzig & Schöner, 2005). Many psychophysical effects occurring in sensorimotor and perceptual decision making tasks provide evidence for these concepts (Wilimzig & Schöner, 2005).

Dynamic Field Theory of Stimulus-Response Associations

To extend DFT to stimulus-response association tasks a concept of the linkage between continuous sensory and motor dimensions is needed. Continuous dimensions may be linked through a multi-dimensional association matrix. Following the DFT concept of neural activation fields based on the Amari equations we use a mathematical formalization by means of multidimensional fields. Mathematically, generalizing the concepts

for one-dimensional fields to the multi-dimensional case is straightforward (Taylor, 1999). Minimally, stimulus-response association requires a two-dimensional field with one sensory (perceptual) parameter, denoted by y , and one motor parameter, denoted by x . This field represents *all potential* associations of a sensory-motor feature through a dynamical equation of the following form:

$$\begin{aligned} \tau \dot{u}(x, y, t) &= -u(x, y, t) + h + S(x, y, t) \\ &+ \int \int w(x, x', y, y') f[u(x', y', t)] dx' dy' \end{aligned}$$

Due to the interaction of global inhibition and local excitation

$$\begin{aligned} w(x - x', y - y') &= -w_{inhibit,xy} \\ &+ w_{excite,x} \exp\left[-\frac{(x - x')^2}{2\sigma_{w,x}^2}\right] w_{excite,y} \exp\left[-\frac{(y - y')^2}{2\sigma_{w,y}^2}\right] \end{aligned}$$

localized peaks can arise for the appropriate input building stable states of activation. Such a localized peak then represents both a feature (perceptual decision) and a response (motor decision) that can be read out for movement planning.

How is the input structured? The two-dimensional fields represent all possible feature-response associations but in a given situation only those linkages that are relevant for the current situation are activated. This is achieved through prior distributions of activation (preshape). Preshape, information about how to respond to certain stimuli like "press the right button for a red stimulus", provides localized activation specifying response parameters for feature parameters, $S_{pre}(x, y, t)$ (see Figure 2). The stimulus itself specifies a feature, for example "red", but does not give any information about the response dimension, $S_{stimulus}(y, t)$, thus the stimulus input is a ridge perpendicular to the motor dimension (see Figure 2).

Preshaped activations are subthreshold as long as there is no stimulus information. The stimulus information acts as a local shift of activation (local for the stimulus dimension, delocalized for the response dimension). With the stimulus input the subthresholded preshape is uplifted enough to generate a stable peak of activation (see Figure 2). This peak generation is strongly driven through interaction dynamics as with the stimulus contribution the localized preshape comes into the competitive regime of local excitation and global inhibition.

Experimental signatures

Distance of choices

A first signature of the importance of the metric structure of task parameters is the finding that the metric distance between choices matters (Erlhagen & Schöner, 2002). When preshapes are close along the feature dimension but specify different motor responses, inputs overlap with more than one preshape (Wilimzig & Schöner, 2005). As the stimulus input thus gives a contribution to more than one possible choice, both choices

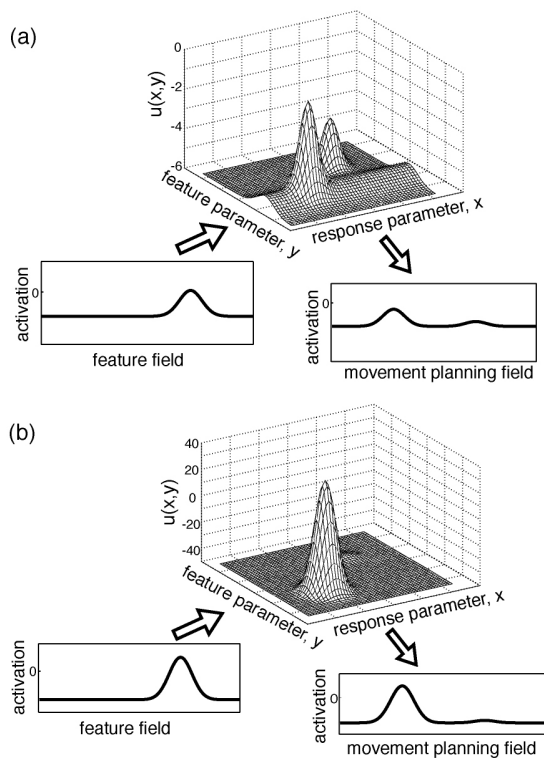


Figure 2: Prior information (preshape) provides localized information specifying values for both dimensions (a). Stimulus information specifies only a value for the feature dimension but is unspecific for the response dimension (a). Due to the interaction single peaks of activation arise reflecting both a feature and a motor decision that can be read out for movement planning (b).

actively compete with each other leading to a substantial amount of inhibition (see Figure 3).

In psychophysical literature this "distance effect" is one of the most robust phenomena in mental comparison paradigms (review by Leth-Steensen & Marley, 2000).

Number of choices

The influence of number of choices as an increase of reaction time for an increasing number of choices is formalized through Hick's law. Erlhagen and Schönner (2002) have shown that the evolution of Hick's law is an inherent consequence of the DFT concept of preshape. Each choice adds a single distribution of preshaped activation. If choices are metrically distant, they interact primarily through inhibitory interaction, thus adding more choices adds more inhibitory interaction to the field slowing down responses to each of the choices.

As interaction is sensitive to metric structure DFT predicts a switch to primarily facilitatory interaction for metrically close choices, thus in the limit case of sufficiently close choices the Hick effect can be reversed as adding more choices then means adding more facilitatory interaction (McDowell et al., 2004).

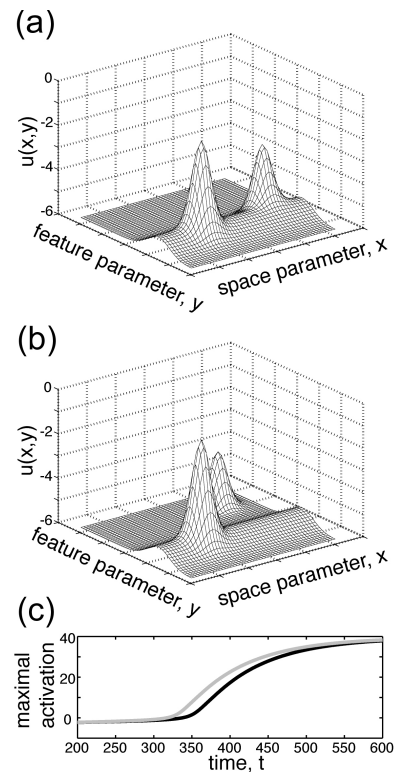


Figure 3: If choices are metrically close along the feature dimension but specify different responses (a), the incoming stimulus overlaps with both choices so they actively compete with each other resulting in a relatively slow response generation ((c), black line). If choices are metrically distant along the feature dimension (b), the stimulus specifies only one of them so the peak generation is faster ((c), grey line).

For stimulus-response association fields DFT thus predicts that for sufficiently distant choices each stimulus-response association adds an inhibitory contribution to the field (Figure 4). In psychophysical literature this is related to the question whether the number of motor responses or the number of stimuli determines reaction time. A classic result is indeed, as predicted by DFT, that the number of stimulus-response associations determines reaction time (Keele, 1986). For sufficiently close choices, for example if similar stimuli are grouped under the same response (multi-to-one mapping), DFT predicts that this effect decreases or even inverts (Figure 4) which is confirmed by experimental data (for example Lacouture, Li & Marley, 1998). Specifically, Pelizzer and Hedges (2003) showed that when subjects had to point toward the location of a target the number of precued locations influences reaction time as predicted by Hick's law. When the subjects had to respond to the target by pressing a button, not the number of precued locations but their metrical distance determined reaction time.

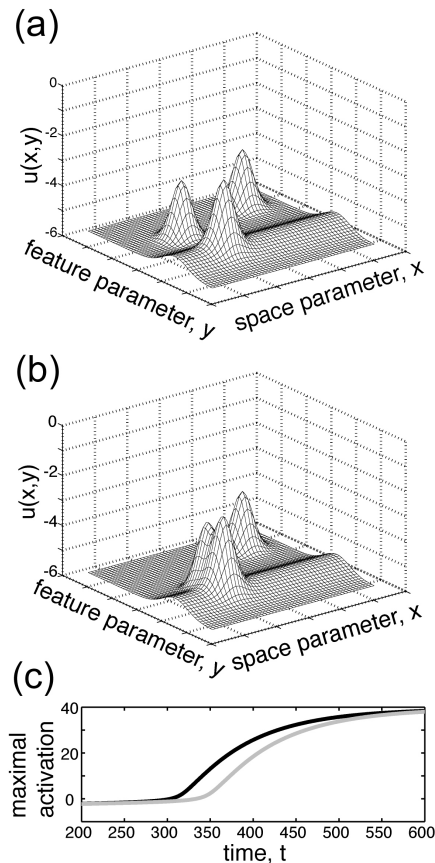


Figure 4: Metrically distant choices (a) interact through inhibitory interaction leading to the classic Hick effect. For metrically close choices – metrically close along the feature dimension, specifying the same response (b) – this can switch to primarily facilitatory interaction leading to much faster response generation for metrically close choices ((c), black line) than for distant ones ((c), grey line), although in both cases the same number of stimulus-response associations is specified.

Distributions of preshaped activation may also result from previous tasks, such as memory traces of previously learned associations. It is a well-known effect that when participants have to switch between two types of associations ("task-switching"), their responses are slower compared to a single task design. Within DFT this effect is due to the inhibitory influence of preshapes resulting from the previously learned associations.

However, DFT predicts that this effect decreases with decreasing metric distance between choices. Having learned similar responses to the same stimulus or the same response to similar stimuli decreases or even inverts the classic task-switching cost. Thus, whether the number of choices, either involved in current processing or previously learned ones, matters depends on their metrical distance.

Probability of choices

The amplitude of preshapes codes for the probability of choices similar to prior probabilities in Bayesian inference – the more probable a choice is the higher the amplitude of the preshape. Thus, if a probable choice is specified through the stimulus contribution, it reaches threshold earlier. On a psychophysical level, this is formalized through the Hyman law referring to faster responses toward more probable choices. DFT predicts that if choices are sufficiently close, they interact through facilitatory interaction, thus less probable choices benefit from the facilitatory interaction of the preshape of the more probable choice. This leads to the prediction that for metrically close choices the Hyman effect disappears which could be confirmed experimentally (McDowell et al., 2002).

Within DFT, the Hyman law is a result of the memory traces of prior activation history (Erlhagen & Schöner, 2002). Repeating the same response in reaction to a repeated presentation of the same stimulus leads to faster reaction times, known as a facilitatory pretrial effect (for a review see Luce, 1986) due to the increased preshape for this choice. Whether responses to other stimuli can contribute from this facilitatory memory trace depends on the metric distance between stimuli and responses respectively. In principle, such an effect was shown on an abstract level shown by Campbell & Proctor (1993). Again, whether the probability of choices matters depends on their metrical distance.

Influence of task environment - manual Stroop task

What kind of evidence exists for the assumption that the representation of the Stroop task is based on similar kinds of representation? Similar as for other stimulus-response paradigms, the distance of choices matters. For the Stroop paradigm this means that the distance determines the amount of interference: If relevant and irrelevant information specify similar, that is metrically close information, the Stroop effect is larger than if they specify dissimilar information (Pavese & Umiltà, 1998, 1999).

In the classic Stroop paradigm participants respond orally which is a highly overlearned response for human adults. In manual Stroop tasks participants have to associate colors with responses toward perceptually marked response locations in the task environment which is an association learned within the course of the experiment. Stimuli are color-words written in different print colors, so the stimulus contains two sources of information: the word information and the print color. If the task is to respond to the word information, in the manual Stroop task the print color causes interference if it is incompatible with the word information which gave rise to the label "reversed Stroop effect" (for example Durgin, 2003) as for the classic word reading task the opposite effect occurs.

Within the DFT model of the manual Stroop effect the association field consists of a feature (color) and a spatial dimension. Response buttons add localized preshaped activations, associating colors with response locations.

Stimulus contributions spread out along the spatial dimension. As two values are specified by the stimulus – one through its color and one through its word information – two inputs are fed into the field that can either specify the same feature value (compatible situation) or different ones (incompatible situation) (see Figure 5).

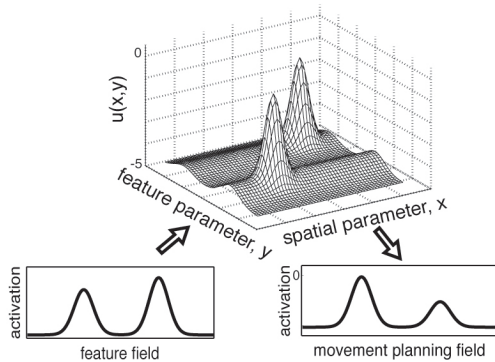


Figure 5: In the manual Stroop task participants communicate their decisions by pressing colored buttons. This task requires a stimulus-response association field with one feature (color) and one spatial dimension (for example movement direction). Localized preshapes reflect information about the location of the response buttons. As the stimulus itself contains two sources of information, for example through its print color and its word information, two stimulus ridges are fed into the field with the respective strengths depending on which information is the relevant and which the irrelevant one.

The manual Stroop paradigm shows that the task environment has an important impact on whether the Stroop effect occurs or not. In the model, inhibition arises mostly through the overlap of the stimulus contribution with a preshape, not through the stimulus itself as it does not specify a response. Thus, DFT predicts that a response option has to be specified for a particular color in order to produce interference. That is, the irrelevant stimulus color has to be present in the set of colors used for the response space. Indeed it was shown that irrelevant information referring to colours used within the experiment lead to a substantially larger amount of interference (Durgin, 2003).

Furthermore, even if the irrelevant information refers to a response option that is part of the current task set, the interaction with the environment has an important impact: The Stroop effect only occurs if the response buttons are visibly labeled, within the field of vision of the subjects and not rearranged between trials (overview by Sugg & McDonald, 1994).

Different sources of information, such as inputs from sensory surfaces and memory traces reflecting recent activation history, thus contribute significantly to stimulus-response associations. Within, DFT all these sources of information are reflected by the amount of preshaped activation.

Discussion

A number of psychophysical effects support the concept that metric descriptions of relevant feature and motor dimension are necessary to explain how nervous systems associate stimuli with responses as predicted by DFT. The manual Stroop effect further indicates that the representation of associations must integrate different sources of information. The concept of preshape in Dynamic Field Theory provides a basis for understanding this integration of current information from sensory surfaces and recent information from previous trials leading to a continuous updating of information about associations.

Within the framework of Dynamic Field Theory, the concept of a memory trace representing the recent history of activation in the field has been used to understand how representations are preshaped by prior experience. This has led to an account for how the action history influences reaching in young infants (Thelen et al., 2001), how choice probabilities determine reaction time (Erlhagen & Schöner, 2002), and how spatial memory becomes biased toward previously memorized locations (Schutte, Spencer & Schöner, 2003). In stimulus-response association tasks the opposite effect of an inhibition of just executed responses may also occur (overview by Luce, 1986). However, recent evidence suggests that this effect might be due to an attentional bias (Fecteau, Bell & Munoz, 2004; Fecteau et al., 2004).

This integration of different sources of information provides an important contribution to the question how the system learns new stimulus-response associations. Learning needs to work on a very fast time scale as human adults are able to learn new associations within very few practice trials or even ad hoc. As Dynamic Field Theory provides a framework of how these different sources of information are integrated, it may serve as an important tool to understand how stimulus-response mappings adjust depending on situational constraints, to explore how learning can work unsupervised on a fast time scale, basically bootstrapping itself from previous responses through preactivations leading to a highly flexible system.

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