

Hysteresis and Phase Transitions when Grasping Objects of Different Sizes

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Abstract

The state of many systems is observed to depend on its previous states, a phenomenon called hysteresis. Experiments on grasping behaviour in humans have found that if subjects are instructed to grasp objects which sequentially increase or decrease in size the size of the object at which the subject switches from one hand to two occurs at a different object size than when the subject switches from two hands to one- i.e., there exists a hysteresis effect in the behavioural transition. In this article we review experimental and theoretical work on these observations, and we briefly discuss how we might try to relate the observed behaviour to activity at the neural level.

I. INTRODUCTION

Many out-of-equilibrium systems exhibit “memory” of the past states of the system, and hence the behaviour of the system as it evolves in time depends strongly on its previous history; the name given to the phenomenon is “hysteresis”. A common example in the field of physics is the magnetization of a magnet in an external field^{1,2}: the magnetization jumps between two different values when the external field is tuned, but the value of the field at which the transition occurs depends on if the field is being increased or decreased. Other known systems which exhibit hysteresis include systems with wetting phenomena³, granular flows⁴, superconductors⁵⁻⁷, among many others.

The focus of this work will be hysteresis observed in behavioural studies. Our primary example is the observation that when humans are instructed to sequentially pick up objects of different sizes, they tend to use one hand for small objects and two hands for larger objects; however, the transition between using one hand or two occurs at different sizes depending on if the subjects pick up objects in order of increasing or decreasing size. This suggests the transition is not induced solely due to biomechanical constraints, such as the box being too large to hold with one hand - there is a perceptual component to the behaviour that determines which of the two grasping modes is invoked. A natural question one might then ask is what is the neural circuitry that underlies the observed behaviour? By studying the behavioural phase transition and the neuron activity during it can we determine constraints on the behaviour of the underlying neural circuitry, and perhaps even develop a neural network-level which gives rise to the behavioural hysteresis transition?

This article is structured as follows: In section II we review experiments that observe hysteresis in this transition, in section III we present the phenomenological theory proposed to describe the behaviour at the qualitative level, and in section IV we discuss experiments that could determine the corresponding neural activity during the behavioural experiment and lead to a neural network-level description of the behaviour. Finally, in section V we summarize the findings to date and speculate what future experiments and theoretical investigations could be undertaken.

II. EXPERIMENTS

Grasping is a very important skill for humans and other primates. The opposable thumb and subsequent ability to grasp objects and make tools has proved invaluable to the development of human society. As such, studying grasping behaviour is of great interest, particularly in light of the fact that of all the animals capable of grasping, humans have evolved the most complex nervous systems (in the sense that we can think, speak and reason about very abstract concepts). It is also of interest to understand how grasping behaviour changes during the developmental stages of childhood^{8,9}.

Experimentally it is found that how a person holds an object depends on the dimensions of the object compared to the dimensions of the person’s own hand^{8,10,11}. In particular, if an object is much smaller than a person’s hand, she will hold it with one hand, but if the object is much larger she will hold it with two hands. When the object is of comparable size with a person’s hand, whether she holds it with one or two hands depends on if she has been primed to use one hand or two. As such, if a person is presented with a sequence of

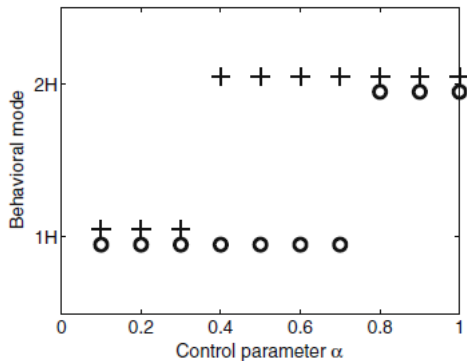


FIG. 1: From Ref. [12]. The control parameter α characterizes the object size to hand size ratio, 1H is the one-handed grasping mode and 2H is the two-handed grasping mode. Hysteresis results as the 1H2H transition occurs at a different value of α than the 2H1H transition.

objects of increasing (decreasing) size, she will initially use one (two) hand(s) to hold the object, and at a critical size of object will switch grasping modes. However, because of the priming effect by initializing the sequence with either a very small object or a very large object, the size of the object at which the transition occurs will be different depending on the initialization condition - that is, there is a hysteresis effect that determines when the one hand-two hand transition occurs, and the condition is different for the two different initial conditions. A schematic representation of the hysteresis is given in Fig. (1).

A. Observation and order of the mode-switching transition

In an experiment involving multiple subjects, the natural variables to plot are the percentage of one (or two)-handed grasps versus the object size. However, the critical object size at which a one-hand to two-hand (1H2H) transition or a two-hand to one-hand (2H1H) transition occurs will generally be different for different subjects, so instead of using object size as a variable, one should instead use a dimensionless control parameter to characterize the experiments in order to eliminate differences between different subjects. In this case the relevant control parameter is the ratio of the characteristic object size to the characteristic hand size^{8,10,11}, labeled α . The exact definition of “object size” and “hand size” depends on the exact details of the experiment. For the experiment of Ref. [8], the objects to be grasped are cubes, and so the characteristic object size may be taken to be the linear dimension of the cube. The characteristic hand size may then be taken to be distance between the thumb and index finger and maximum extension (roughly the width of a grasp). A plot of percentage of one handed grasps versus object size and the control parameter α is shown in Fig. (2) for children of ages five, seven and nine. We see that the data plotted against the control parameter α are nearly along a single curve, suggesting a potentially universal transition regardless of age.

Fig. (2) appears to indicate that the transition to a two-handed mode is continuous; however, this turns out to be an artifact of grouping together all of the data, including subjects with slightly different values of the transition parameter α_c . Normalizing the object

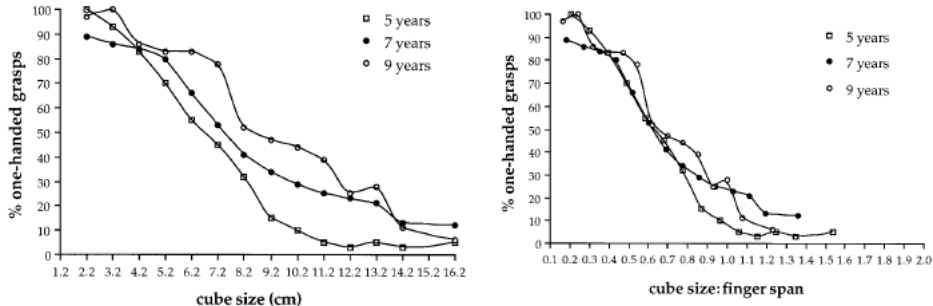


FIG. 2: From Ref. [8]. Left: Plot of Percentage of One-Handed grasps versus object size. Right: Plot of Percentage of One-Handed grasps versus control parameter α . All points are averages over several subjects at each value of the object size or α .

size by each individual’s finger grasp was not sufficient to eliminate all differences between subjects. This supports the suggestion that the mechanism behind the transition is not solely based on biomechanical limitations. Other sources of difference are likely due to differences in perception of the subjects regarding how big each object is, hence leading to slightly different values of α_c for each individual. If one instead groups together data with respect to the transition point a discontinuous transition is found to fit the data better than a continuous transition¹³.

B. Hysteresis

We now discuss the observation of hysteresis. In the experiments of Ref. [8] the value of α at which the 1H2H and 2H1H transitions occur are indeed found to be clearly different in 82% of the experiments. For the increasing sequences of object sizes the transition was found to occur at a mean (taken over all subjects) α_{c1} of 0.98 ± 0.18 , while for decreasing object sizes the transition is found to occur at a mean α_{c2} of 0.62 ± 0.29 . The experimenters find that the interaction of age and sequence is not significant, suggesting that in most subjects hysteresis is present regardless of age. Fig. (3) shows the results of the experiment. Because the data of all subjects was used in the analysis, the discontinuity in the 1H2H and 2H1H jumps is not visible.

Hysteresis has been observed in similar grasping experiments. In Ref. [11] subjects are instructed to decide if they would pick up a plank presented to them using either one or two hands (the subjects are not actually instructed to pick up the plank so as to avoid inducing any pressure on the subject which could alter the results). The experimenters find hysteresis in the percentage of perceived two-handed grasps depending on if the planks are presented in increasing or decreasing order. They also tested presenting the planks in a random order and found that the resulting percentage versus α curve falls roughly inside the hysteresis curve.

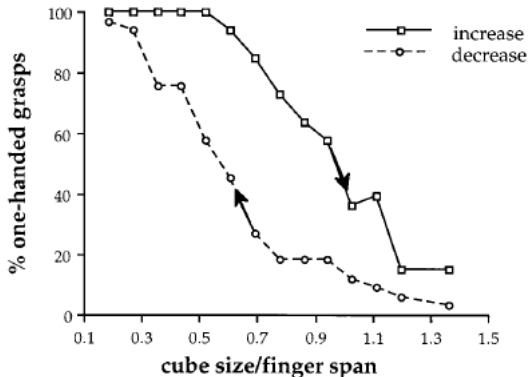


FIG. 3: From Ref. [8]. Plot of the mean percentage of one-handed grasps versus α for both increasing and decreasing sequences, clearly showing hysteresis. The arrows indicate the transitions, which gives the $\alpha_{c1} = 0.98$ and $\alpha_{c2} = 0.62$ values quoted in the text.

III. THEORY

Having described the experimental observation of hysteresis in the transition between behavioural modes of the grasping experiments, we now turn to modeling the transition theoretically. In principle we would like to be able to write down a neuron-level model that we can relate to the observed behaviours and exhibits the experimentally observed behaviours. However, this is at present beyond our abilities, so we would instead like to develop a phenomenological model that exhibits the transition. What properties must our model have? The system is driven out of equilibrium, so we must consider time-dependent dynamics, leading us to consider a dynamical systems model. Because we want to describe a phase transition, we would like our model to describe the dynamics of an order parameter which is zero during one of the grasping modes and non-zero in the other. In order to have hysteresis, we need a competition between the two behavioural modes, so we will define two order parameters, one for each mode. For the system of equations to exhibit hysteresis we need at least two fixed points, one for each behavioural mode. This requires a nonlinear system of equations. We also require the only stable fixed points have one of the order parameters zero and the other non-zero; any other fixed points must be unstable, or the model will describe behavioural modes not observed experimentally.

The authors of Ref. [12] propose the following system of equations for the order parameters of the one-handed and two-handed grasping modes (ξ_1 and ξ_2 , respectively):

$$\begin{aligned} \frac{d}{dt}\xi_1(t) &= \lambda_1\xi_1 - B\xi_2^2\xi_1 - C(\xi_1^2 + \xi_2^2)\xi_1, \\ \frac{d}{dt}\xi_2(t) &= \lambda_2\xi_2 - B\xi_1^2\xi_2 - C(\xi_1^2 + \xi_2^2)\xi_2. \end{aligned} \quad (1)$$

The equations are adapted from a theory of pattern recognition proposed by H. Haken¹⁴, which has also been used to describe oscillations in the perception of ambiguous patterns¹⁵. The amplitude ξ_1 (ξ_2) is the order parameter of the one-handed (two-handed) mode, and

is restricted to being positive. However, the magnitude of the order parameters, for the purposes of this discussion, is irrelevant. We are only concerned with the order parameter being zero (i.e., the mode corresponding to the order parameter is not activated) or non-zero (the mode corresponding to the order parameter is in use). For instance, $(\xi_1, \xi_2) = (0, 1)$ or $(0, 17)$ both describe the two-handed grasping mode. The parameters λ_1 and λ_2 are “attention parameters” (the name is inherited from the use of the parameters in the pattern recognition theories), and are allowed to be negative or positive. A negative attention parameter is interpreted to indicate a biomechanically forbidden mode (e.g., a large box being too heavy to hold with one hand would be indicated by $\lambda_1 < 0$). The parameters B and C couple the modes together and are restricted to being positive.

The choice of terms in Eq.’s (1) is simply to satisfy the mathematical requirements of the model, and do not necessarily have an *a priori* physical interpretation. The first term on the right hand side serves to increase (decrease) the amplitude if its attention parameter is positive (negative). The second term is an interaction term; when ξ_1 grows, for example, it tends to reduce ξ_2 , and vice versa. The last term provides two kinds interaction terms in each equation of motion, one of the same form as the second term and another of the form ξ_i^3 , which ensures the order parameter remains bounded: if the order parameter starts to grow large, the ξ_i^3 term will act to reverse the increase.

It is shown in Ref. [12] that the system exhibits four fixed points. Two fixed points represent the one-handed grasping and two-handed grasping modes. Only these fixed points may be stable. The other fixed points correspond to the no-activity mode and coexistence of the two grasping modes, and neither fixed point is ever stable. The one-handed (two-handed) mode has a fixed point $(\xi_1^*, 0)$ $((0, \xi_2^*))$, where

$$\xi_1^* = \sqrt{\frac{\lambda_1}{C}}, \quad \xi_2^* = \sqrt{\frac{\lambda_2}{C}}. \quad (2)$$

When $\lambda_1 > 0$ and $\lambda_2 \leq 0$ ($\lambda_2 > 0$ and $\lambda_1 \leq 0$) the one-handed mode (two-handed mode) is stable, while the other does not exist. When both attention parameters are positive, both fixed points exist. Defining $g \equiv 1+B/C$, one finds that the one-handed (two-handed) mode is stable when $\lambda_2/\lambda_1 < 1/g$ ($\lambda_2/\lambda_1 > g$) while the other is unstable, and when $1/g < \lambda_2/\lambda_1 < g$ both modes are stable and the fixed point the system converges to in the long time limit depends on which basin of attraction the system is initialized in. This is the feature of the model which gives rise to hysteresis.

As discussed earlier, when the attention parameters are negative we interpret this as a biomechanical constraint which physically prevents activation of the grasping mode. When both attention parameters are positive but one mode is unstable, the mode could still in principle be performed but is not the preferred mode: for example, one could pick up a small pebble with both hands, but it is quite an awkward endeavour. Similarly, one could lift a large but light box with just one hand, but it might become tiring to do so very quickly! The situation in which both modes are bistable corresponds to the perceptual ambiguity in which the subject maintains the initial mode of behaviour as there is no perceived advantage to switching modes.

So far the model has not made use of the experimental control parameter α . We introduce

this now by modifying the parameters λ_1 and λ_2 to depend on α . The parameters B and C may in principle also depend on α , but for simplicity the authors of Ref. [12] consider only the variation of the attention parameters, and so we follow their discussion here. However, before doing so, we note that if we were not to follow Ref. [12] and allow B to depend on α , then if it were to happen that B vanished at one of the critical values of α , then $g = 1$ and both critical values would be equal to one another: $\alpha_{c1} = \alpha_{c2}$. Accordingly, the hysteresis has vanished! However, this appears to be a *very* finely tuned condition, and so it seems that B will not vanish at α_c unless we have some additional parameter that can be used to tune B such that it $B(\alpha_c) = 0$. If there were some other experimental parameter we could tune such that $B(\alpha_c) = 0$ then this effect could be achieved. Evaluating ξ_1^* and ξ_2^* at α_c (as would be calculated below) we find that the amplitudes are non-zero at the transition point, and hence the transition is still discontinuous. Accordingly, there are no critical exponents associated with the 1H2H transition. This concludes our discussion of the possibility of tuning B , we and now return to following the discussion of Ref. [12].

The simplest modification we can make to the λ 's is to make them linear functions of α ,

$$\lambda_1 = \lambda_1^0 - \beta\alpha, \quad \lambda_2 = \lambda_2^0 + \beta\alpha, \quad (3)$$

where $\lambda_1^0 > \lambda_2^0$ and chosen such that $\lambda_1, \lambda_2 > 0$. The condition $\lambda_1^0 > \lambda_2^0$ ensures that as $\alpha \rightarrow 0$ the system will at best be in the bistable region, and will accordingly converge to the one-handed fixed point, as desired. The signs preceding β were chosen in light of experimental observations that λ_1 must decrease as α increases (i.e., the one-handed mode becomes less stable as the object size grows). The parameter β does not necessarily have to be the same for both attention parameters, but for simplicity it is assumed to be.

Using the critical conditions $\lambda_2(\alpha_{c1})/\lambda_1(\alpha_{c1}) = 1/g$ (corresponding to the two-handed mode becoming unstable) and $\lambda_2(\alpha_{c2})/\lambda_1(\alpha_{c2}) = g$ (corresponding to the one-handed mode going unstable), one finds

$$\alpha_{c1} = \frac{1}{\beta(1+g)} (\lambda_1^0 - g\lambda_2^0), \quad \alpha_{c2} = \frac{1}{\beta(1+g)} (g\lambda_1^0 - \lambda_2^0). \quad (4)$$

The authors of Ref. [12] solved the system of equations (1) numerically using Eq. (3) and found that as α was increased (decreased) ξ_1 (ξ_2) vanished at α_{c2} (α_{c1}) while ξ_2 (ξ_1) became non-zero, confirming the analytic calculations. A plot of ξ_1, ξ_2 showing the hysteresis loops for each is shown in Fig. (4). We see immediately that the transition is first order, and that the transitions occur at different values of α .

The solution of Eq.'s (1) represent the result of an experiment on a single subject. As shown in the previous section, the critical values α_c vary for different individuals. To better match the results of a large number of trials we suppose that only the parameter B , for simplicity, is a random variable over different subjects such that the critical values α_c have a distribution of values. Note that α_{c1} and α_{c2} are related to one another in this model by

$$\alpha_{c1} = \beta^{-1}(\lambda_1^0 - \lambda_2^0) - \alpha_{c2}; \quad (5)$$

hence the two parameters cannot have different functional distributions, only different mo-

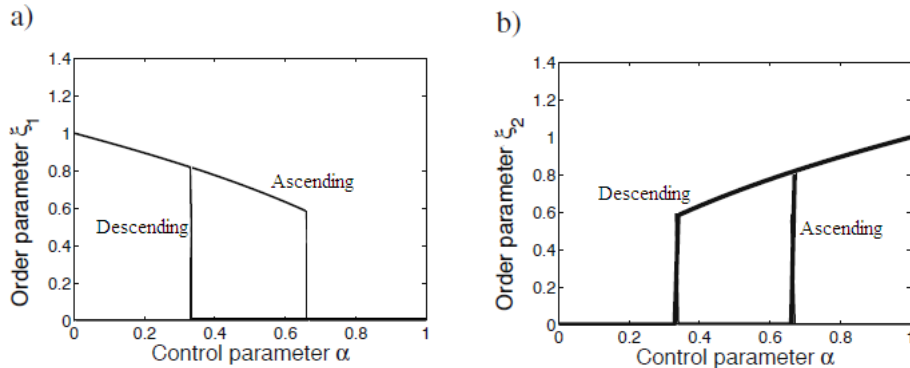


FIG. 4: Adapted from Ref. [12] to clearly show the hysteresis curves for ξ_1 and ξ_2 . In plot a) as α is increased ξ_1 follows the “ascending” curve until α_{c2} , at which point it vanishes. If α is then decreased ξ_1 remains zero until α_{c1} , at which point ξ_1 jumps up the “descending” line. For plot b) as α is decreased ξ_2 follows the “descending” curve until α_{c1} , at which point it vanishes. If α is then increased ξ_2 remains zero until α_{c2} at which point it jumps up the “ascending” line. Curves are numerical solutions of Eq.’s (1) with attention parameters as given by Eq. (3). Plotted curves represent the long time limit of the order parameters (i.e., the fixed points). Parameters chosen by the authors of Ref. [12] are as follows: $B = C = 1$, $\lambda_1^0 = 1$, $\lambda_2^0 = 0$, $\beta = 1$; accordingly, $g = 2$, $\alpha_{c1} = 1/3$ and $\alpha_{c2} = 2/3$. For the increasing (decreasing) case, α was increased (decreased) in steps $\Delta\alpha = 0.01$. Eq.’s (1) were solved a forward Euler method with $\Delta t = 0.1$ with a total of 10000 iterations for every α . The α_c ’s at which the transitions were observed to occur correspond to the theoretically predicted values.

ments related by Eq. (5). Each branch of the hysteresis curve looks like

$$\xi_i^*(\alpha) = \sqrt{\frac{\lambda_i^0 \pm \beta\alpha}{C}} \Theta(\pm(\alpha - \alpha_c)),$$

where the \pm signs are $(-)$ if $i = 1$ and $(+)$ if $i = 2$, the critical value α_c is α_{c1} on the “descending” branches of the hysteresis curves and α_{c2} on the “ascending” branches and $\Theta(x)$ is the Heaviside step function. Averaging over these curves will give the hysteresis curve for a large number of trials; however, recall that the amplitudes ξ_i are not what we measure experimentally (the physical interpretation of them is not even clear, so we don’t even know *what* to measure). What one actually measures is the percentage of one (or two)-handed grasps of the objects, so in considering the observed experimental hysteresis loops we can dispense of the prefactor out front of the step function in doing our average.

The result of averaging over the step function is just $1 - F(\alpha)$ for ξ_1 and $F(\alpha)$ for ξ_2 , where $F(\alpha)$ is the cumulative distribution function of the random variable α_c . For illustrative purposes, we assume that α_c is Gaussian distributed. This is not technically correct, as α cannot be negative, but as long as μ is sufficiently above zero and σ is sufficiently small the probability of a negative value of alpha will be negligible and a Gaussian distribution will be approximately valid. We plot the resulting percentage of one-handed grasps versus

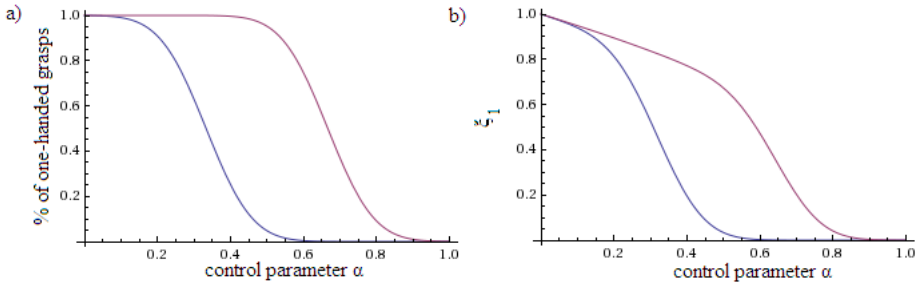


FIG. 5: a) Plot of % of one-handed grasps versus α . b) Plot of ξ_1 , the order parameter for one-handed grasps, versus α . The blue (purple) curve corresponds to “descending” (“ascending”) values of α . Parameters used are the same as in Fig. (4). The means are $\bar{\alpha}_{c1} = 1/3$, which implies $\bar{\alpha}_{c2} = 2/3$ given the chosen parameters. The standard deviation is chosen to be $\sigma = 0.1$.

α (along with the average $\xi_1^*(\alpha)$ for comparison) in Fig. (5). Comparing plot a) of Fig. (5) with Fig. (3) we find that they qualitatively, but not quantitatively, agree.

IV. DETERMINING THE NEURONAL BASIS OF THE BEHAVIOUR

Underlying every behaviour is a series of neural connections whose dynamics give rise to the observed behaviour. Understanding the dynamics of the neurons that underly certain behaviours would help us better understand both the observed behaviours and how our neural circuitry works and generates collective properties like behaviour or thought. Understanding how neural circuitry gives rise to behaviour, and what observed behaviour tells us about neural circuitry, could be very important to understanding some neurological disorders such as Schizophrenia¹⁶ or Parkinson’s disease¹⁷, the neurological development of individuals with other disorders such as Down’s syndrome¹⁸, developing brain-machine control devices¹⁹, how observing the behaviour of others influences our own behaviour²⁰, and countless other endeavours.

We would like to understand the neural processes behind the hysteresis in the described grasping experiments. To date, we are not aware of any studies which have investigated neural processes during the exact experiments described in this work, but fMRI measurements of brain activity during other grasping experiments have been performed^{21,22}. The authors of Ref. [21] used functional magnetic resonance imaging (fMRI) to study human neural activity in the human analogue of a neural circuit known to be associated with grasp-related sensorimotor transformations in macaques. Single neuron studies in the macaques suggest that grasp related behaviour is related to hand configuration, so the experiments of Ref. [21] study the activity in this circuit when humans grasp, using visual (i.e., perceptual) cues, spheres of two different sizes with two different kinds of grasps, as shown in Fig. (6). The experiments also tested the effect of grasping an object with an unnatural type of grasp, i.e., grasping a small object with a whole hand grasp or a large object with a precision grasp (definition of the grasps is shown in Fig. (6)). The fMRI images display the neuron activity during an experiment; the graph shows how changing the size of the object or type of

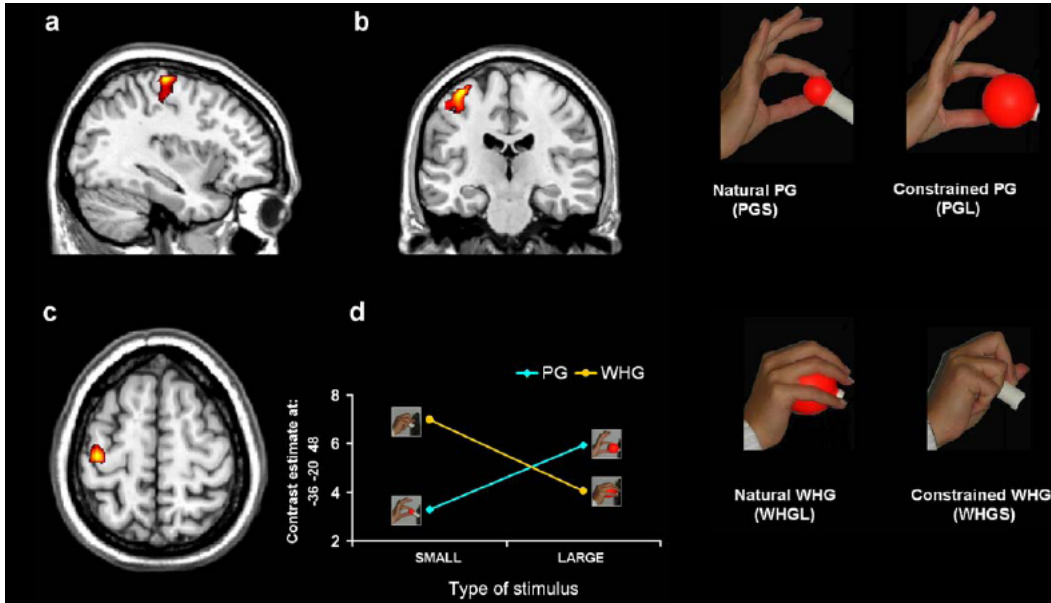


FIG. 6: From Ref. [21]. Highlighted areas on the brain scans correspond to active areas during the experiment, with level of activity indicated by contrast. The graph shows how the activity changed with ball size and type of grasp. Grasps defined by pictures on the right of the figure.

grasp altered neural activity (as shown by contrast of the highlighted regions on the fMRI images). These are the results most relevant to our present discussion: how does grasping different-sized objects and the type of grasp used affect neural activity? The experiments find two regions that appeared to be most active when mismatched grasps were performed. Because the transition between one and two-handed grasps occurs when there is a mismatch between the perceived size of the object and the number of hands used, we may expect the same (or a similar) neural circuit to be involved in 1H2H/2H1H transition.

V. SUMMARY AND FUTURE WORK

Let us now review the significance of what we have discussed and conclude with some discussion of future work. We described a set of experiments in which hysteresis was observed during a transition from one-handed to two-handed grasping of various sizes of objects. To describe the experiments mathematically we analysed a simple model proposed in Ref. [12]. The goal of the model was to exhibit a discontinuous mode-switch transition associated with hysteresis. As shown, these features were realized in the model: the dynamical system (1) exhibits two stable fixed points, that depend on the control parameter α , which poses a regime of bistability in which hysteresis is possible. The model qualitatively captures these results seen in the experiments, but quantitative agreement is lacking. This is not surprising, however, as the model is only a simple model proposed to capture the desired features of the experiments; is not an actual model intended to represent the actual physical situation. However, if we can identify the physical analogues of the parameters $\lambda_{1,2}(\alpha)$, B and C

then we could in principle fit experimental measurements of the parameters as functions of experimental variables to include in the model to achieve a more accurate understanding of the experiments, similar to the use of phenomenological Landau theory in physics to study phase transitions. By investigating how the critical parameters $\alpha_{c1,2}$ change as experimental variables are tuned we could determine $\lambda_{1,2}$ and β . Furthermore, if by tuning different experiment variables we discovered a continuous transition then we might be able to derive critical exponents or scaling functions that should be universal and hence compared quantitatively to experimental measurements.

To connect the output of the model with the experimental observations, which are averaged over many subjects, we assumed that the critical transition parameters α_c are random variables. This allows us to average over the order parameter hysteresis curves to study the results of many trials, as in Fig. (5) b). However, we do not actually measure the order parameters in the experiment; we actually measure the percentage of one or two-handed grasps. To calculate this curve we do not actually need a model - we can just assume there are two transitions at α_{c1} and α_{c2} , which are distributed about different means, and average over the one-subject hysteresis curve (as in Fig. (1)) to produce Fig. (5) a). However, without the model we would not have a definite relation between the critical parameters α_{c1} and α_{c2} and could not relate their means or show that their distributions must have the same functional form (though it seems natural to assume this).

The main success of the model is the existence of two mutually exclusive behavioural modes which become bistable in a certain regime of the parameter space of the model, giving rise to hysteresis as a function of a control parameter, α , as observed experimentally. The mathematical features of this simple model are thus expected to be essential features of any improved model of the observed behaviours. An obvious extension of the model would be the inclusion of a stochastic noise source in Eq.'s (1). A noise source could induce transitions between the one and two-handed grasping modes, effectively shifting the critical control parameter α_c and potentially even changing the order of the transition. Further refinements could be the inclusion of more experimentally tunable variables, as mentioned above, or order parameters for different behavioural modes not explored in these experiments.

Ideally, we would like to construct a neuron-level model which we could relate to the experimentally observed behaviours. Such a model could, for example, be driven by an input signal, corresponding to visual information about the size of the object, which is transmitted through a neural network model which outputs a response signal that would correspond to actuating either a one-handed grasp or a two-handed grasp depending on the input (which in turns depends on perceived environmental properties such as the size of the object). Though such a model is not necessary to produce an improved version of Eq.'s (1) it would further our understanding of the connections between the neural and behavioural levels of cognition. Furthermore, if an effective model such as Eq.'s (1) could be derived from the neuron model, then because the degrees of freedom of neural network model represent the properties of actual neurons it would have the advantage of telling us what the actual physical analogues of the order parameters ξ_i and model parameters $\lambda_{1,2}$, etc., are in the model. In the current macroscopic model of Eq.'s (1) we have no obvious way of identifying these parameters with physically measurable quantities.

To this end, experiments such as the one described in section IV are important for de-

termining which neural circuits are involved in human behaviours. Studies of the identified neural circuits may then reveal the relevant properties that should be included in an accurate neural network model of the behaviour dynamics.

In conclusion, in this work we presented results of behavioural experiments which observe a phase transition between two behavioural modes of grasping which depend on the ratio of the size of the object being grasped to the characteristic hand size of the subject. We then presented a model that has been proposed to capture the qualitative features of the experiments. We discussed how one might go about improving the model to make it quantitatively more accurate and how experiments measuring neural activity during behavioural experiments could help with the development of neural-level models which could then be related to the behavioural model and the relevant parameters to be measured experimentally could then be identified. The brain is a complicated system, so relating neural dynamics to behaviour will not be an easy task. It is thus important to devise well-posed questions to study experimentally and theoretically in order to uncover the fundamental principles behind behaviour and cognition.

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